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## INTRODUCTION

An increasing number of zoologists, both resident and foreign, have become interested in the herpetology of Suriname. In view of this it seems advisable to summarize our knowledge of various groups of Suriname's amphibians and reptiles. On the other hand, with the current rapid development of the country and the concomitant increase in exploration, it would be premature to attempt faunistic monographs of any segment of the herpetofauna. As a compromise, therefore, I present this survey of the tree frogs (Hylidae and Centrolenidae) of Suriname. The purpose of this synopsis is to place on record the 29 species of tree frogs now known from Suriname<sup>2</sup>, and to provide an aid to their identification.

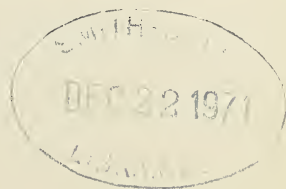
The two families of tree frogs occurring in Suriname (Hylidae and Centrolenidae) may be distinguished from other Suriname frogs by the presence of intercalary cartilages—flat, disk-like cartilages between the distal and penultimate phalanges of the fingers and toes. The paradoxical frogs (Pseudidae) have an extra cartilage in the same location in the digits, but the extra cartilage is rod-like rather than disk-like. The centrolenids can be distinguished from the hylids by the terminal cartilage in the digits, which is T-shaped in the former, and claw-shaped in the latter group.

Politically Suriname is divided into seven districts: Suriname, Brokopondo, Commewijne, Coronie, Marowijne, Nickerie, and Saramacca (see fig. 1). Geographically it is low and swampy in the north where it meets

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<sup>2</sup>Since this manuscript was submitted for publication Hoogmoed [1969, Zoologische Mededelingen 44(5): 75-81] has reported the Guianan hyliid *Allophryne ruthveni* Gaige from several localities in Suriname.

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the Atlantic Ocean, but the southern third is rather mountainous. Julianatop (1280 m.) in the Wilhelmina Mountains is the highest point. A dam for the production of electrical power has been built on the Suriname River at Afobaka, Brokopondo, impounding a lake approximately seventy-five kilometers in length.

In the accounts of species below, I cite each name, as originally proposed, and the first use of the current combination. This is followed by a diagnosis intended to distinguish the species of Suriname tree frogs. I have not attempted to refine these diagnoses to the point of distinguishing Suriname species from forms occurring elsewhere. For the purpose

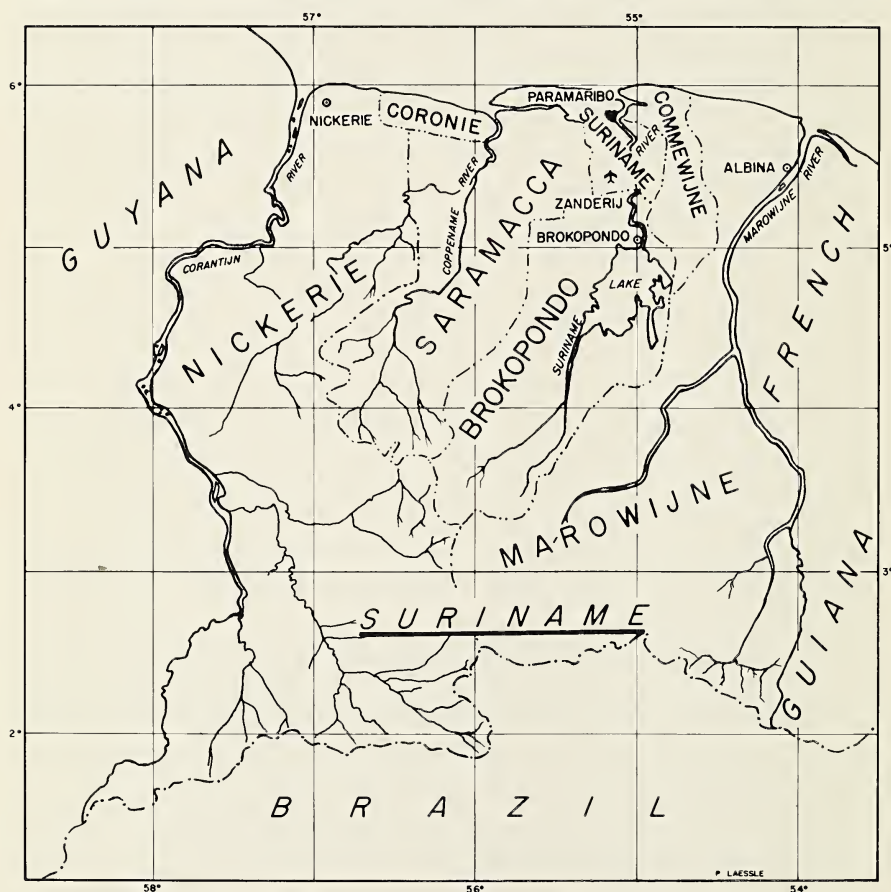


Fig. 1. Map of Suriname showing the districts, major cities, and major drainage systems.



of this list I think it is more important, for example, to distinguish *Hyla rubra* from other species of Suriname frogs than to distinguish it from the various varieties of *rubra* and its allies throughout South America. The diagnosis is sometimes followed by a short discussion. Each account concludes with a list of all Suriname specimens I have examined.

#### ACKNOWLEDGMENTS

In the course of this work I have, as usual, become indebted to many people. For the privilege of examining specimens in their charge I wish to thank Dr. Leo D. Brongersma and Dr. M. Boeseman of the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Dr. Dirk Hillenius and S. Dann, Zoölogisch Museum, Amsterdam (ZMA); Miss Alice G. C. Grandison, British Museum [Natural History (BMNH)]; Dr. Jean Guibé, Muséum National d'Histoire Naturelle, Paris (MNHN); Dr. Charles M. Bogert and Dr. Richard G. Zweifel, American Museum of Natural History (AMNH); Dr. Ernest E. Williams, Museum of Comparative Zoology, Harvard (MCZ); Neil D. Richmond and Dr. C. J. McCoy, Carnegie Museum (CM); Dr. Walter Auffenberg, Florida State Museum (FSM); Edmond V. Malnate, Academy of Natural Sciences, Philadelphia (ANSP); and Dr. Charles A. Reed, formerly of Yale Peabody Museum (YPM). Specimens bearing my field numbers are identified by the initials CJG. Dr. D. C. Geijskes of Surinaams Museum, Paramaribo (SM) not only allowed me to examine that museum's material, but introduced me to the country and took me on my first collecting trip there. Dr. P. Bolwerk, Walter Polder, Sgt. H. Pijpers, and Murray de la Fuente of Paramaribo (now associated with Carnegie Museum) were extremely helpful in ways too numerous to mention. Dr. Duvall Jones, Steven Bass, and my wife, Olive B. Goin, all were diligent and helpful field companions. Drs. M. S. Hoogmoed reviewed the entire manuscript for me to my great benefit. The map and figure are from the pen of Paul Laessle. Funds to travel to Suriname and to provide time in Gainesville for the study of the material were made available by the National Science Foundation (GB-3644). To all of these and others not mentioned I am indeed most grateful.

#### SYSTEMATIC PROBLEMS

In a number of the species listed below (*i.e.*, *Hyla leucophyllata*, *H. crepitans*, *H. rubra*, and *Osteocephalus taurinus*) the Suriname populations differ from populations I have seen from other localities, and in

many cases these geographic populations surely merit nomenclatorial recognition. While I have pointed out differences in some of the cases of which I am aware, I have refrained from applying names simply because I do not believe anything is to be gained at the present time by applying trinomials to populations studied in faunistic surveys of political divisions. It seems to me preferable to wait until each species is studied throughout its entire range before defining and naming the vicarious populations worthy of recognition.

New names have been proposed for Suriname tree frogs sixteen times. Ten of these are today considered valid species. These are *Hyla boesemani*, *H. fuentei*, *H. leucophyllata*, *H. marmorata*, *H. proboscidea*, *H. rubra*, *Phyllomedusa bicolor*, *P. hypochondrialis*, *Centrolenella geijskesi* and *C. taylori*. The present status of the other six nominal species is discussed below.

*Hyla doumercii* Duméril and Bibron, 1841:551. The type in the Paris Museum (MNHN 766) has been examined, and surely is nothing more than a *Hyla crepitans*, as used in this paper.

*Hyla indris* Cope, 1871:555. I have not seen this type but the description leaves little room for doubt that this is another synonym of *H. crepitans* as used here.

*Hyla levaillantii* Duméril and Bibron, 1841:550. When I examined this type (MNHN 764) I reached the conclusion that it was most likely a half-grown specimen of *Osteocephalus taurinus*. It should be compared directly with freshly preserved young individuals of the latter species from Suriname, however, before a definite synonymic assignment is made.

*Hyla frontalis* Daudin, 1803:24. Although the type of this species (MNHN 4868) is somewhat the worse for wear, there is no question whatsoever that it is a perfectly good *H. leucophyllata*.

*Hylella cappelli* Lidth, 1904:94. As I have reported elsewhere (Goin, 1964) direct comparison of this type (RMNH 4463) with a paratype of *Centrolenella fleischmanni* indicates that they are one and the same.

*Phyllomedusa scleroderma* Cope, 1868:112. The type of this species (ANSP 2173) has been examined. It is simply a fine large specimen of *P. bicolor*.

In addition to the six names listed above that are not now recognized as valid species, Lidth (1904) used two names, now in current use, for Suriname frogs. *Hyla fasciata* as he used it certainly refers to *Hyla calcarata* as used here. *H. fasciata*, with its type locality in the Andes of



Ecuador, possibly represents a western race of the eastern *H. calcarata*. At any rate, as pointed out by Cochran and Goin (1970:208), the differences between the two are of such a magnitude that synonymizing them is inadvisable.

In the same paper Lidth also referred to some specimens from Suriname as *Hyla leprieuri*. I was unable to locate any specimens of this species in the Rijksmuseum collections, nor have I seen any specimens of this species from Suriname in any other collections.

#### KEY TO THE TREE FROGS OF SURINAME

In the key and diagnoses, the term *small* refers to species generally under 30 mm. snout-vent length in breeding adults, *medium* to species between 30 and 60 mm. in snout-vent length, and *large* to species above 60 mm. in snout-vent length.

1. Terminal phalanges T-shaped ..... 2  
Terminal phalanges claw-shaped ..... 4
2. No vomerine teeth present ..... 3  
Vomerine teeth present ..... *Centrolenella geijskesi*
3. Dorsum white or yellowish in preservative ..... *C. fleischmanni*  
Dorsum with lavender spots in preservative ..... *C. taylori*
4. Pupil of eye vertical ..... 5  
Pupil of eye horizontal ..... 7
5. Distinct vertical dark bars on the posterior surfaces of the thighs ..... 6  
No distinct vertical dark bars on the posterior surfaces of the thighs ..... *Phyllomedusa bicolor*
6. First toe shorter than second ..... *P. tomopterna*  
First toe longer than second ..... *P. hypochondrialis*
7. Male with paired vocal pouches; skin on top of head tough and thick  
or skin on top of head thin, but under the skin the top of the skull  
exostosed ..... 8  
Male with median single vocal pouch; skin on top of head thin and  
top of skull smooth ..... 9
8. Top of skull smooth, but skin on top of head  
thick and tough ..... *Phrynohyas venulosa*  
Top of skull exostosed (except in immature females), skin on top  
of head thin ..... *Osteocephalus taurinus*
9. Palpebral membrane of eye distinctly reticulated ..... 10  
Palpebral membrane clear ..... 11
10. Fingers fully webbed; webbing between fingers and toes  
dark gray to black ..... *Hyla maxima*  
Fingers but half-webbed; webbing between fingers and toes  
not dark gray to black ..... *H. geographica*

11. Dorsum bright green to pale yellowish green in life, milky white  
to dirty white in preservation .....12  
Dorsum with some type of pattern, not uniform green .....15
12. Snout rounded; no distinct dark stripe along snout .....13  
Snout distinctly pointed; a dark stripe from tip of  
snout to eye .....*Sphaenorhynchus eurhostus*
13. No small, triangular dermal appendage on heel .....14  
A small, triangular dermal appendage on each heel .....*H. albomarginata*
14. Vomerine teeth in two small, rounded patches; size medium .....*H. punctata*  
Vomerine teeth in two arched series; size medium to large .....*H. fuentei*
15. Dorsal pattern present or absent, not brilliantly contrasting white  
on brown, thighs and ventral surfaces not pink .....16  
Dorsal pattern of brilliant enamel white on chocolate brown  
(see fig. 2), ventral surfaces pink .....*H. leucophyllata*
16. Dermal spine absent from heel, or if present low and triangular .....17  
An elongated dermal spine on heel .....*H. calcarata*
17. A low, triangular dermal spine on heel .....18  
Heel without a dermal appendage .....19
18. A triangular fleshy proboscis at tip of snout .....*H. proboscidea*  
Snout pointed, but without a fleshy proboscis at its tip .....*H. acuminata*
19. Belly surface immaculate or nearly so .....20  
Belly heavily spotted with discrete, rounded, coal-black spots ....*H. marmorata*
20. When the upper arm is held at right angles to the body, a  
triangular fold of skin, the patagium, stretches across the  
axillary region from the side of the body to the base of the arm .....21  
No patagium present .....24
21. No dark triangle on the dorsum .....22  
A distinct, hollow triangle in the middle of an ovate pink area  
the most conspicuous mark on the dorsum .....*H. ornatissima*
22. Dorsum pale or mottled, but lacking scattered tiny round white spots .....23  
Dorsum dark gray with scattered, rather tiny but distinct,  
white spots .....*H. boesemani*
23. Size small, vomerine teeth in two small, rounded  
patches .....*H. microcephala misera*  
Size medium, vomerine teeth in two somewhat arched series ....*H. megapodia*
24. Vomerine teeth in two small, rounded series .....25  
Vomerine teeth in two rather heavy, arched series .....27
25. Two horizontal white lines on the heels match up with a similar  
white line above the vent when the heels are flexed .....*H. minuta*  
No white lines on heels and above the vent .....26
26. Posterior face of thighs patterned with very distinct, squarish,  
vertical black marks .....*H. eglei*  
Posterior surface of thighs either immaculate or with scattered  
orange and black vermiculations .....*H. rubra*

27. Fingers with but a trace of web at base .....28  
 Fingers one-third to one-half webbed .....*H. faber*  
 28. No more than two phalanges of longest toe free of web .....*H. crepitans*  
 Nearly three phalanges of longest toe free of web .....*H. multifasciata*

### ACCOUNTS OF SPECIES

#### *Hyla acuminata* Cope

*Hyla acuminata* Cope, 1862:354.

TYPE LOCALITY: "Paraguay."

DIAGNOSIS: A medium-sized tree frog with tiny dermal appendages on the heels, with vertical dark bars on the posterior surfaces of the thighs, without reticulations on the palpebral membranes, and with the toe webs nearly black.

It is distinguished from *H. egleri* by its larger size (*H. egleri* = 25-30 mm. snout-vent) and by the tiny dermal heel appendages; from *H. geographica* by the lack of reticulations on the palpebral membranes; from *H. calcarata* by its dermal heel appendages, which are short and inconspicuous instead of being long and conspicuous; and from *H. proboscidea*, which it really resembles most, by the absence of the fleshy proboscis on the snout.

SPECIMENS EXAMINED: *Suriname*: RMNH 13047, BMNH 66.9.20.20, no specific locality, Marowijne: RMNH 13044, Nassaugebergte, Km. 12.9. *Suriname*: BMNH 1946.4.2.18-23, Republiek.

#### *Hyla albomarginata* Spix

*Hyla albomarginata* Spix, 1824:33, pl. 8, fig. 1.

TYPE LOCALITY: "Bahia."

DIAGNOSIS: A medium-sized tree frog, green in life but nearly white in preservative, with triangular dermal heel appendages and ulnar and tarsal ridges on the forearms and feet, respectively.

The green (or white) coloration sets off *H. albomarginata* from all other *Suriname* tree frogs except *Sphaenorhynchus eurhostus*, *Hyla fuentei*, and *H. punctata*. The definite ulnar and tarsal folds along the outer side of the arms and legs serve to separate it from them.

SPECIMENS EXAMINED: *Suriname*: RMNH 1894 (3), no specific locality.

#### *Hyla boesemani* Goin

*Hyla boesemani* Goin, 1966a:229.

TYPE LOCALITY: "Suriname, Suriname District, near Zanderij."

DIAGNOSIS: A small-to-medium-sized tree frog with a small but well-developed patagium, a dorsal pattern of scattered light spots on a gray background, and uniform gray thighs without a pattern.

It differs from all the non-green *Hyla* of *Suriname* that approach 30 mm. snout-vent length, except *H. leucophyllata*, by the absence of pattern on the thighs. It differs strikingly from *H. leucophyllata* in dorsal pattern and in that the thighs, though without a pattern, are nonetheless pigmented.



SPECIMENS EXAMINED: *Suriname*: Nickerie: YPM A1351, Kayser Airstrip. *Suriname*: AMNH A75555, BMNH 1966.26, CM 41595, 50471-50473, MCZ 52833, USNM 159140, Onverwacht; CM 50553, Onverwacht-Zanderij Road; RMNH 12601 (holotype), 12602-12603, CJG 2408-2409, CM 50492, FSM 22367, Zanderij.

### *Hyla calcarata* Troschel

*Hyla calcarata* Troschel, 1848:660.

TYPE LOCALITY: "British Guiana."

DIAGNOSIS: A medium-sized *Hyla* with long, pointed dermal appendages on the heels, with the toe webs black, and without reticulated palpebral membranes.

It differs from *H. maxima* in lacking palpebral reticulations, and in having dermal heel appendages. It differs from *H. geographica* in lacking palpebral reticulations and in having the toe webs black. It differs from *H. marmorata* in the presence of dermal heel appendages and the absence of a patagium.

SPECIMENS EXAMINED: *Suriname*: Brokopondo: RMNH 11471, near Brokopondo; RMNH 4468 (2), Toekoemoetokreek. *Coronie*: SM (unnumbered), Coppenameweg. *Suriname*: CM 50584, Powakka.

### *Hyla crepitans* Wied

*Hyla crepitans* Wied, 1824, pl. 47, fig. 1.

TYPE LOCALITY: "Tamboril, Jiboya, and Areal de Conquista, Bahia, Brasil."

DIAGNOSIS: A medium-to-large tree frog without dermal appendages on the heels and without reticulations on the palpebral membranes. At least the two distal phalanges of the outer three fingers are free of web.

It can be distinguished from *H. maxima* and *H. geographica* by the absence of palpebral reticulations, from *H. calcarata* by the absence of dermal heel appendages, and from *H. multifasciata* by the dark-brown stripe through the nostril and eye of the latter. It is perhaps most easily confused with *H. faber*, but *H. crepitans* has the fingers webbed only at the base, while *faber* has the fingers one-third to one-half webbed.

NOTES: Although I call the *Suriname* frogs *Hyla crepitans*, they certainly differ from Colombian specimens with which I am familiar. They are smaller in size, paler, do not have conspicuous thigh patterns, and have less webbing between the fingers. In life the ventral color was a bright orange-yellow. This species, like *Hyla rubra*, needs study throughout its range, and defining of the different geographic races.

SPECIMENS EXAMINED: *Suriname*: RMNH 9624-9625, Railroad Km. 54.5; AMNH 76305, BMNH 66.9.20.18, RMNH (unnumbered), no specific locality. Brokopondo: RMNH 17, Brokopondo; SM (unnumbered), Kabel. *Coronie*: SM (unnumbered), Coppenameweg, Km. 7. Marowijne: RMNH 863, 1046, Wanekreek. *Saramacca*: ZMA (unnumbered), Hendriktop. *Suriname*: CM 50572, Onverwacht; CM 50552, Onverwach-Zanderij Road; AMNH 5098, RMNH 1867, near Paramaribo; CM 44219-44221, 44227-44237, 44240-44245, Powakka; BMNH 1946.4.2.45, CM 50486-50491, SM (unnumbered), ZMA 5913, Zanderij.

*Hyla egleri* Lutz

*Hyla egleri* Lutz, 1968:8.

TYPE LOCALITY: "Belem, Para, Brazil."

DIAGNOSIS: A small (25-30 mm.) *Hyla* with conspicuous bright, vertical black bars on the posterior surfaces of the thighs and without tiny dermal appendages on the heels and the tip of the snout.

It differs from *H. proboscidea* by its smaller size (*H. proboscidea* = 35-40 mm. snout-vent) and by lacking a dermal appendage on the tip of the snout. It also differs from *H. acuminata* in being smaller (*H. acuminata* = 35-40 mm. snout-vent), in having the posterior thigh marking conspicuous rather than inconspicuous, and in lacking tiny, pointed dermal appendages on the heels.

SPECIMENS EXAMINED: *Suriname*: Suriname: CM 50500-50501, 50573, near On-verwacht; CM 44238-44239, Powakka; CJG 2421, CM 50493-50498, 50558, Zanderij.

*Hyla faber* Wied

*Hyla faber* Wied, 1821:519.

TYPE LOCALITY: "Brazil, Fazenda de Aga between Itapemirim and Irititaba Rivers; St. Agnes, Bahia, and along the coast."

DIAGNOSIS: A large *Hyla* without reticulations on the palpebral membrane, without dermal heel appendages, and with the fingers one-third to one-half webbed.

The lack of palpebral reticulations separates it from *H. maxima* and *H. geographica*, the lack of heel appendages distinguishes it from *H. calcarata*, and the presence of distinctly webbed fingers sets it off from both *H. crepitans* and *H. multifasciata*.

NOTES: This is the only tree frog reported here of which I have not seen a Suriname specimen. It surely is part of the fauna, though, for Dr. M. Boeseman took a picture of a typical *H. faber* nest and its included eggs on March 5, 1964. This nest was on Grankreek about four or five miles upstream from where it empties into the Suriname River. The site is now covered by Toekomstig Stuwmeer. Specimens should be diligently sought throughout Brokopondo. As the voice of a singing male is said to be loud and metallic, reminiscent of a blacksmith pounding an anvil, these have come to be known as blacksmith frogs.

*Hyla fuentei* Goin and Goin

*Hyla fuentei* Goin and Goin, 1968:581.

TYPE LOCALITY: "Suriname, Suriname District, Powakka."

DIAGNOSIS: A medium-to-large *Hyla*, dark, waxy green in life but fading to a dirty white in preservative. The fingers are webbed at the base and there is no trace of mottling on the dorsum or crossbands on the legs.

In life it is distinguished from all Suriname tree frogs except *Phyllomedusa bicolor* by its size and bright-green coloration. From *Phyllomedusa* it differs in having a horizontal rather than a vertical pupil. In preservative *H. fuentei* would most likely

be distinguished from *P. bicolor* by the lack of dorsal pattern and crossbars on the legs.

SPECIMENS EXAMINED: *Suriname*: Brokopondo: FSM 27038, Lands Bosbeheer Kamp 8 Road. *Suriname*: CM 44218 (holotype), Powakka.

*Hyla geographica geographica* Spix

*Hyla geographica* Spix, 1824:15, fig. 1.

*Hyla geographica geographica*, Parker, 1935:511.

TYPE LOCALITY: "Tefe, Amazonas, Brazil," according to Bokermann, 1966:51.

DIAGNOSIS: A medium-sized *Hyla* with the palpebral membrane reticulated, and with dermal appendages on the heels.

It differs from *H. maxima*, the only other *Suriname* tree frog with reticulated palpebral membranes, in having small, triangular, dermal heel appendages, in having pale rather than dark webs between the toes, and in being medium-sized rather than large.

SPECIMENS EXAMINED: *Suriname*: ZMA 6021, no specific locality. Brokopondo: CM 50581, Brownsberg. Marowijne: USNM 159023-159024, Paloemeu. Nickerie: CM 44222, Kabalebo R., near airstrip.

*Hyla leucophyllata* (Beireis)

*Rana leucophyllata* Beireis, 1783:182, pl. 11, fig. 4.

*Hyla leucophyllata*, Gravenhorst, 1829:31.

TYPE LOCALITY: "Suriname."

DIAGNOSIS: A small-to-medium-sized tree frog with spectacular pattern and coloration. In life, chocolate brown dorsally with a superimposed pattern of pale-gold markings, and with the thighs and ventral surfaces brilliant pink. In preservative the dorsal ground color remains chocolate brown, the dorsal markings become enamel white and the thighs and ventral surfaces fade to flesh color.

The brilliant pattern at once sets off *H. leucophyllata* from any other *Suriname* frog.

NOTES: Topotypes of *H. leucophyllata* from *Suriname* are remarkably uniform in dorsal pattern (fig. 2). In all but a few specimens the distribution of the dorsal white areas is as follows: a triangular area on top of the head that is continuous across the upper eyelids, with broad dorso-lateral stripes ending just posterior to the region of the sacral hump; a longitudinally oriented ovate blotch on the midline of the back that extends anteriorly from just above the vent and terminates anterior to the sacral hump between the dorso-lateral bands described above; a white spot on each elbow, forearm, and the lateral side of each hand; a small, round spot on each knee; an elongated blotch that covers practically the entire dorsal surface of the shank and has a shallow notch on its inner margin about the midpoint of its length; and one or two small spots on the lateral side of each foot.



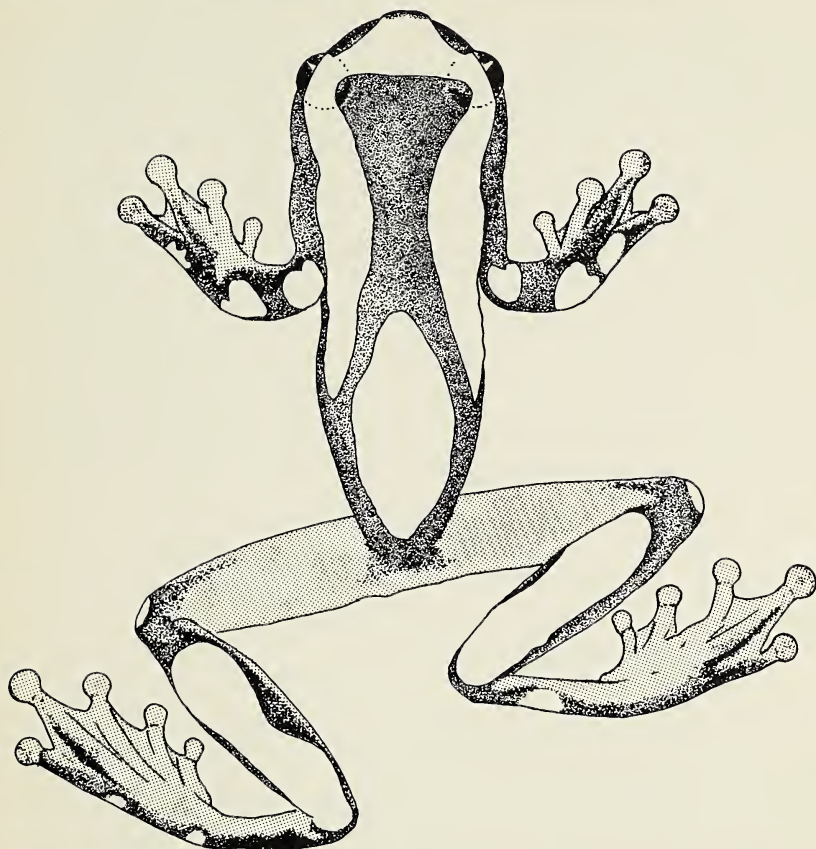


Fig. 2. *Hyla leucophyllata* (CM 50555) from Zanderij, showing the dorsal pattern of typical *H. leucophyllata*. Paul Laessle, del.

In the specimens from Suriname I have examined, I have seen but two noteworthy variations. In one specimen (RMNH 3606) the dorsolateral light stripe on the right side of the body is in contact with the suprapelvic light spot. In three individuals [RMNH 1837 and 1848 and MNHN 4868 (type of *H. frontalis*)] the shank spots are divided into two spots on each leg, and in two individuals (RMNH 3606 and 4420) the shank spots are divided on one leg but not on the other.

SPECIMENS EXAMINED: *Suriname*: BMNH 66.8.14.265-267, MNHN 4868 (holotype of *H. frontalis*), RMNH 1848 (3), 2814, 4642, 18374, no specific locality. Commewijne: RMNH 3606, Wiawiabank Lijn Km. 9.2. Marowijne: CJG 2001, Wiawiabank Lijn Km. 23.8. *Suriname*: RMNH 4420, Coronieweg Km. 2.5; RMNH (unnumbered), Paramaribo; CJG 2475, CM 50555, Zanderij.

*Hyla marmorata* (Laurenti)

*Bufo marmoratus* Laurenti, 1768:29.

*Hyla marmorata*, Daudin, 1803:34.

TYPE LOCALITY: "Suriname."

DIAGNOSIS: A small-to-medium-sized frog, with well-developed webs on the fingers, and a well-developed patagium. The throat, belly, and ventral surfaces of the thighs are yellow, with a profusion of small, rounded black spots. The under side of the forearms, hands, shanks, and feet are black. The proximal portion of the finger and toe webs are black, and distal portions are bright yellow.

The combination of finger webs, patagium, and ventral coloration will immediately distinguish this from any frog now known from Suriname.

SPECIMENS EXAMINED: *Suriname*: SM (unnumbered), Wilhelminagebergte; USNM 12550, no specific locality. Brokopondo: RMNH (unnumbered), Afobaka. *Saramacca*: ZMA (2 unnumbered), Hendriktop. *Suriname*: AMNH 77451, Joden-savanna, Kamp 8; CM 44202-44212, Powakka; BMNH 1946.4.2.44, Zanderij.

*Hyla maxima* (Laurenti)

*Rana maxima* Laurenti, 1768:32.

*Hyla maxima*, Günther, 1858:99.

TYPE LOCALITY: none given.

DIAGNOSIS: A large *Hyla* with reticulated palpebral membranes and dark webbing between the toes.

It differs from *H. geographica*, the only other tree frog in Suriname with reticulated palpebral membranes, by its larger size and by having the toe webs dusky-to-black rather than pale.

SPECIMENS EXAMINED: *Suriname*: SM (unnumbered), Karujs 3; AMNH 76298-76299, ZMA 6022, no specific locality. Brokopondo: RMNH (unnumbered), Afobaka; CM 50582, Brownsberg; SM (unnumbered), Sarakreek; RMNH (unnumbered), no specific locality. Marowijne: RMNH (unnumbered), Apoemavallen, Marowijne R.; RMNH (unnumbered), Grancoela-eiland; USNM 159026, Paloemeu. Nickerie: RMNH (unnumbered), Boven, Nickerie R.; SM (unnumbered), Coeroni-eiland; RMNH (unnumbered), Lucie R.; CM 44213, Mataway, 10 miles upstream from Cowval, Corantijn R.; SM (unnumbered), Sipaliwini; RMNH 9699, "oeverbos langs rivier." *Saramacca*: RMNH (unnumbered), Hebiweri; ZMA (2 unnumbered), Hendriktop; RMNH (unnumbered), Linker Coppename R., Wilhelminagebergte; RMNH 1766, 1768, 1872, 1876-1877, 5392, 6040-6041 (plus several unnumbered), Tibiti Basiskamp; RMNH 5931, Tibiti, Km. 2.1. *Suriname*: ZMA 5912, Zanderij.

*Hyla megapodia* Miranda-Ribeiro

*Hyla megapodia* Miranda-Ribeiro, 1937:67 (the illustration and name without description were published in Miranda-Ribeiro, 1926, pl. 5, fig. 5).

TYPE LOCALITY: "Mato Grosso, Brazil."

DIAGNOSIS: A medium-sized tree frog with a dorsal pattern of mottling, with a brown stripe from the nostril through the eye to the tympanum, without a white line above the vent, and without heel spurs.

It is most similar to *H. crepitans* and *H. multifasciata*, but it differs from both of these in lacking the transverse white line above the vent.

NOTES: Because of the absence of distinct, postfemoral dark vertical bars and the extension of the web of the fourth toe to middle of the penultimate phalanx, I use the name *H. megapodia* rather than the more familiar *H. raniceps* for these specimens. The largest specimen (RMNH 11469) shows a striking similarity to Miranda-Ribeiro's (1926, pl. 5, fig. 5) figure of this species. The smaller specimens are somewhat dry and shrunken, but are certainly the same species.

The identification of these specimens as *H. megapodia* was originally made by the late Dr. Doris M. Cochran of the United States National Museum.

SPECIMENS EXAMINED: *Suriname*: RMNH 13045-13046, "3rd Kamp, Km. 14.9, zitsbos"; RMNH 11468, no specific locality. *Marowijne*: RMNH 11469-11470, Wanekreek N. *Saramacca*: RMNH 11467, Rechter Coppename R.

### *Hyla minuta* Peters

*Hyla minuta* Peters, 1872:680.

TYPE LOCALITY: "near Rio de Janeiro."

DIAGNOSIS: A small frog with reduced webs between the fingers and reduced pattern on the thighs. The dorsal pattern of most specimens from Suriname consists of a broad dark band between the eyes and one or two similar dark bands across the back. A white transverse line above the vent coincides with similar lines on the heels when the legs are flexed.

The transverse white line above the vent and on the heels distinguishes this from the other small local hylas that have reduced patterns on the thighs: *H. boesemani*, *H. leucophyllata*, and *H. microcephala misera*.

SPECIMENS EXAMINED: *Suriname*: AMNH 7630, no specific locality. *Suriname*: CM 50469-50470, Onverwacht; BMNH 1946.4.2.46-47, CM 50557, ZMA 5914 (5), Zanderij.

### *Hyla microcephala misera* Werner

*Hyla misera* Werner, 1903:252.

*Hyla microcephala misera*, Fouquette, 1968:324.

TYPE LOCALITY: "Caracas, Venezuela."

DIAGNOSIS: A small tree frog with reduced pattern on the thighs and dorsum, and without a transverse white line above the vent and on the heels.

It can be distinguished from *H. boesemani* and *H. leucophyllata* by the lack of dorsal pattern, and from *H. minuta*, which may have a reduced dorsal pattern, in lacking the white line above the vent and on the heels.



SPECIMENS EXAMINED: *Suriname*: Suriname: CM 50554, Onverwacht-Zanderij Road; CJC 2388-2389, CM 50474, Paramaribo; CM 50479-50483, Zanderij.

*Hyla multifasciata* Günther

*Hyla multifasciata* Günther, 1858:101, pl. 8, fig. D.

TYPE LOCALITY: "Para."

DIAGNOSIS: A medium-to-large tree frog, slender in build, with reduced webbing between the fingers, and a transverse white line above the vent. A dark-brown stripe passes along each side of the face from the nostril to the eye and thence posteriorly through the tympanum. There is no pronounced pattern, either on the dorsum or on the thighs. There are no dermal heel spurs.

The dark-brown face stripe and the lack of dermal heel spurs will distinguish it from all Suriname frogs of the same general appearance except *H. megapodia*, from which it differs in having a transverse white line above the vent.

NOTES: I follow Cochran and Goin (1970:191-192) in using the binomial *H. multifasciata* for this species. It may well be, as Rivero (1961) points out, that *H. boans* (of Latreille) in the south, *H. lanciformis* in the west and north and *H. multifasciata* in the north and east are nothing more than geographic races of a single wide-ranging species. I feel, however, that we need studies of the entire species (or species group) throughout its range before we begin definitive assignments of trinomials to geographic populations. I have not studied *H. boans*, but I have observed that *H. multifasciata* differs from *H. lanciformis* of Colombia by being much smaller and more slender, lacking the conspicuous dark crossbars on the dorsum and thighs, and in having less webbing between the toes.

In life *H. multifasciata* from Suriname is dark yellow on the top of the head and dorsum, and light yellow on the sides. Some have a few small coal-black flecks on the back. Pigment on the thighs is restricted to the dorsal surfaces only. The supra-anal stripe is bright yellow.

SPECIMENS EXAMINED: *Suriname*: BMNH 66.9.20.16-17, 70.3.10.70, 1936.12.3.-115, RMNH 1885, RMNH (unnumbered), no specific locality. Marowijne: CM 50571, Albina; RMNH 1261, Jai Kreek. *Suriname*: ZMA (unnumbered), "Kolonial Institute"; CM 50550-50551, Onverwacht-Zanderij Road; BMNH 1946.4.2.26, Paramaribo; CM 50576, Zanderij.

*Hyla ornatissima* Noble

*Hyla ornatissima* Noble, 1923:291.

TYPE LOCALITY: "Meamu, Mazuruni R., British Guiana."

DIAGNOSIS: A small-to-medium-sized *Hyla* with a small patagium, and with a dorsal pattern of a distinct dark triangle in the middle of the back, lying in a large, ovate pink area.

The dark triangle in the ovate pink area in the middle of the back conspicuously sets this off from any other Suriname frog.

NOTES: This seems to be a frog of the northern slopes of the Guiana Highlands. I have now seen four specimens of this rare species: BMNH 1905.11.141-142 from Tung district, 2000 feet, Upper Potaro River, Guyana; AMNH A13491, the holotype, from Meamu, Mazaruni R., Guyana; and the specimen from Brokopondo.

Lutz (1951:321), to the best of my knowledge, is the only one who has published a comment on this species since its description. On the basis of the description and a photograph of the type, she suggested that it is possibly allied to *Hyla granosa*. The four specimens I have seen are quite uniform in pattern. The most conspicuous elements of the pattern; present in all specimens, are the dark triangle on the back that lies in the middle of a large pink spot, and the narrow brown stripes, bordered by pink, on each canthus.

SPECIMENS EXAMINED: *Suriname*: Brokopondo: RMNH 4859, Corantijn Escarp., Gran Rio.

### *Hyla proboscidea* Brongersma

*Hyla proboscidea* Brongersma, 1933:267.

TYPE LOCALITY: "in Lager am oberen Gran Rio, Suriname."

DIAGNOSIS: A medium-sized (35-40 mm.) tree frog with conspicuous broad black vertical bars on the posterior surfaces of the thighs, and a small but conspicuous dermal appendage on the tip of the snout.

It is distinguished from *H. acuminata* by the presence of the dermal proboscis, and by having the markings on the posterior surfaces of the thighs conspicuous. It is distinguished from *H. egleri* by its larger size (*H. egleri* does not exceed 30 mm. snout-vent) and by the presence of the dermal proboscis.

NOTES: There are three closely allied species in this group known from Suriname: *H. proboscidea*, *H. acuminata*, and *H. egleri*. Despite their superficial resemblance they are easily distinguished as follows:

*H. proboscidea*—Adults 35-40 mm. snout-vent length; a dermal proboscis on tip of snout; tiny but distinct pointed dermal appendages on heels; broad, vertical dark bands on posterior surfaces of the thighs very conspicuous; known only from the slopes of the mountains on the upper Paloemeu River and the Gran Rio.

*H. acuminata*—Adults 35-40 mm. snout-vent length; no dermal proboscis on snout; small distinct appendages on the heels; broad, vertical dark bars on posterior surface of thighs not particularly conspicuous; apparently widespread north of the mountains.

*H. egleri*—Adults 25-30 mm. snout-vent length; no dermal appendages on snout or heels; broad vertical dark bands on back of thighs very conspicuous; at present known in Suriname only from the upper coastal plain.

SPECIMENS EXAMINED: *Suriname*: RMNH 12517, no specific locality. Brokopondo: ZMA 5710 (holotype), Upper Gran Rio.

*Hyla punctata* (Schneider)

*Calamita punctata* Schneider, 1799:170.

*Hyla punctata*, Daudin, 1803:41.

TYPE LOCALITY: "America."

DIAGNOSIS: A medium-sized, green, tree frog with reduced webbing between the toes and with scattered red spots on the back, in life, though these may fade in preservative. When preserved, the entire individual is likely to fade to plain white.

In Suriname the only hylids other than *H. punctata* that are bright green in life and fade to white in preservative are *Sphaenorhynchus eurhostus* and *H. fuentei*. *H. punctata* is distinguished from the former by having a rounded, rather than a pointed nose, and by the absence of a dark stripe from the nostril to the eye. *H. punctata* differs from the latter in its smaller size, rounded rather than pointed snout, and by having the teeth on the roof of the mouth in small, round patches rather than in long, arched series.

SPECIMENS EXAMINED: *Suriname*: BMNH 66.9.20.21, 70.3.10.71, RMNH 2262A, USNM 11151, 124590, no specific locality. Marowijne: ZMA 5915, Albina; AMNH 62884-62887, Moengo. Saramacca: ZMA (unnumbered), Hendriktop. *Suriname*: CJG 2494, Onverwacht; RMNH 1905, 1911 (2), (2 unnumbered), Paramaribo; CM 50556, Zanderij.

*Hyla rubra* Daudin

*Hyla rubra* Daudin, 1802:19.

TYPE LOCALITY: "Suriname."

DIAGNOSIS: A small-to-medium sized frog of the lowlands with reduced webbing between the fingers, dorsolateral light stripes bounded by stripes of a darker hue, and scattered yellowish spots on the rear of the thighs. These spots may be faint in specimens from the lower coastal plain.

The thigh pattern, dorsolateral light stripes, and size immediately distinguish this frog from all others in Suriname. This is certainly the most numerous of the small tree frogs in the vicinity of Paramaribo.

NOTES: On examination, the series of Suriname specimens is readily divisible into two groups—one from the lower coastal plain and one from the upper.

Those from the lower coastal plain are much paler, and in only one of the specimens is there any semblance of mottling on the thighs. In this individual (a very large female) it consists of no more than a few pale reticulations on the posterior surface of the thigh just proximal to the knees. In the other specimens from this area the thighs are pale, and without any evidence of pattern.

The six specimens at hand from the upper coastal plain are quite dark, and each has well-developed yellowish-white spots surrounded by dark reticulations on both the posterior and anterior surfaces of the



thighs. A single specimen (CM 50574) from near Onverwacht (close to the edge of the lower coastal plain) is as pale as specimens from the lower coastal plain, but has the well-developed thigh pattern typical of upper coastal plain *H. rubra*.

All the specimens from Paramaribo have pale dorsolateral stripes extending from the eye to the region of the groin on each side, bordered above and below by stripes of a darker hue. These bordering dark stripes are not so apparent in those from the upper coastal plain, because of the general darker ground color of the specimens.

Because there are definitely two different populations in Suriname, because the type locality is simply "Suriname," and because no less than fourteen names have been applied to various populations of *H. rubra*, the precise determination of the *forma typica* becomes significant. On the basis of probability it seems likely that Daudin's specimens came from the vicinity of Paramaribo, the major seaport. *H. rubra* is abundant there, and rather rare in the upper coastal plain. It should be mentioned, too, that the type of *H. rubra* was collected before the railroad made exploration of the upper coastal plain convenient. Finally, Daudin's comment that the dorsolateral stripes were "pale ash color" is indicative that he had specimens from the lower coastal plain population. Therefore, I hereby definitely restrict the type locality of *Hyla rubra* Daudin to the vicinity of Paramaribo, Suriname District, Suriname.

SPECIMENS EXAMINED: *Suriname*: RMNH 9665, Railroad Km. 62, RMNH (3 unnumbered), "Suriname Coastal Plain"; RMNH (unnumbered), "G. O. Wagenin-gen"; AMNH 4020, 4022, BMNH 66.8.14.261, 66.8.14.263, 66.8.14.307, RMNH 1898 (7), 1907, 4906 (3), no specific locality. Brokopondo: SM (unnumbered), Kabel; BMNH 1946.4.2.38-40, near Saramacca R., Km. 91.5. Marowijne: RMNH 2393 (2), Albina; USNM 159022, Paloemeu. Nickerie: SM (unnumbered), Corantijn R., Wotonobovallen. Saramacca: RMNH (unnumbered), Voltzberg; RMNH (3 unnumbered), Wanica. *Suriname*: ZMA (unnumbered), "Kolonial Institute"; RMNH (unnumbered), Lelydorp; CM 50574, Onverwacht; AMNH 74456-74469, BMNH 1946.4.2.27-37, CM 44216, 44247, 50475-50478, 50565, RMNH 1911 (8), RMNH (22 unnumbered), USNM 158948-158950, ZMA 5916 (6, plus 6 unnumbered), Paramaribo; CM 44214-44215, 44246, Powakka; CM 44224, Uitkijk; ZMA 6017, Zanderij; SM (18 unnumbered), Zanderij savanna.

### *Phrynohyas venulosa* (Laurenti)

*Rana venulosa* Laurenti, 1768:31.

*Phrynohyas venulosa*, Cochran and Goin, 1970:328-329.

TYPE LOCALITY: Restricted by Duellman (1956:35) to "Lago Teffe, at the mouth of Rio Teffe where it empties into the Rio Solimões, Amazonas, Brasil."

DIAGNOSIS: A large, thick-skinned frog in which the male has paired vocal pouches.

It may be distinguished from other Suriname frogs by its tough, thick skin on top of the head and from all except *Osteocephalus taurinus* by its paired vocal pouches. It differs from *O. taurinus* in having the skin on top of the head thick and tough, and in having the top of the skull smooth.

SPECIMENS EXAMINED: *Suriname*: RMNH (unnumbered), "Dist. Ben"; RMNH 1590, 3rd Kamp, Km. 19.5; RMNH (unnumbered), "Wageminger"; AMNH 76300-76303, BMNH 70.3.10.68-69, RMNH 1852-1853, 1872(3) 1875(5), 1908, (plus numerous unnumbered), no specific locality. Brokopondo: RMNH (unnumbered), Brokopondo; SM (5 unnumbered), Kabel. Coronie: RMNH 4414, Coronieweg. Marowijne: RMNH 8547, 9439 (plus unnumbered), Nassaugebergte. Nickerie: SM (unnumbered), Coeroeni-eiland; CM 44257-44258, 50578, five miles above Oreala, Guyana. Saramacca: ZMA 6018 (plus 5 unnumbered), Hendriktop. *Suriname*: RMNH 13048, Botanical Garden; ZMA (unnumbered), "Kolonial Institute"; RMNH (unnumbered), Lelydorp; AMNH 4009, 77452-77454, BMNH 1946.4.2.24-25, CM 44223, 44225, 44259-44262, 50560, RMNH 1911, SM (three unnumbered), ZMA 5920, Paramaribo; CM 50575, junction Paranam-Zanderij Roads; RMNH (unnumbered), Republiek; SM (unnumbered), Zanderij.

### *Osteocephalus taurinus* Steindachner

*Osteocephalus taurinus* Steindachner, 1862:77.

TYPE LOCALITY: "Rio Negro, Brasil."

DIAGNOSIS: A large, slenderly built tree frog that has the skin on top of the head rather thin and the top of the skull rough and bumpy (exostosed) rather than smooth. The vocal pouches are paired.

It may be distinguished from all the tree frogs now known from Suriname by the exostosed skull, and from all except *Phrynohyas venulosa* by the paired vocal pouches of males.

NOTES: The single specimen I have seen alive from Suriname was heavily speckled on the throat, as are specimens I have seen from Guyana (BMNH 1905.11.120). It was pointed out earlier (Cochran and Goin, 1970:321) that specimens from eastern South America differ in some respects from those in the western part of the range.

I have examined the type of *Hyla levaillantii* Duméril and Bibron in the Paris Museum (MNHN 764), and as noted above I suspect it is a half-grown *O. taurinus*. It should be reexamined with this in mind, and directly compared with freshly preserved *O. taurinus* from Suriname.

SPECIMENS EXAMINED: *Suriname*: BMNH 70.3.10.67, RMNH 1851, 1873-1874 (plus unnumbered specimens), no specific locality. Brokopondo: RMNH (unnumbered), Afobaka. Marowijne: RMNH (2 unnumbered), Jai Kreek; RMNH 8183 (5), RMNH (8 unnumbered), Nassaugebergte, USNM 159025, Paloemeu. Saramacca: RMNH (unnumbered), Linker Coppename R., SM (unnumbered), Tafelberg, Kappelsavanna; RMNH (unnumbered), Tibiti R. *Suriname*: CM 44217, 44226, Powakka; CM 50568, Zanderij Kreek.

*Phyllomedusa bicolor* (Boddaert)

*Rana bicolor* Boddaert, 1772:19.

*Phyllomedusa bicolor*, Wagler, 1830:201.

TYPE LOCALITY: "Suriname."

DIAGNOSIS: A large tree frog with vertical pupils, with the first toe shorter than the second, and without vertical dark bars on the posterior surface of the thighs.

It is distinguished from *P. hypochondrialis* by having the first toe shorter than the second, and from *P. tomopterna* by the absence of vertical dark bars on the posterior surface of the thighs.

SPECIMENS EXAMINED: *Suriname*: AMNH 23937, ANSP 2173 (holotype of *P. scleroderma*), RMNH 1854-1855 (plus unnumbered specimens), no specific locality. Nickerie: SM (unnumbered), Coeroni-eiland. *Suriname*: CM 50569, Zanderij.

*Phyllomedusa hypochondrialis hypochondrialis* (Daudin)

*Hyla hypochondrialis* Daudin, 1803:29.

*Phyllomedusa hypochondrialis hypochondrialis*, Rivero, 1961:150.

TYPE LOCALITY: "Suriname."

DIAGNOSIS: A medium-sized frog with vertical pupils, the first toe longer than the second, and with vertical dark bars on the posterior surfaces of the thighs.

It is distinguished from *P. bicolor* by its smaller size, by having the first toe longer than the second, and by the presence of vertical dark bars on the posterior surfaces of the thighs. It differs from *P. tomopterna* in having the first toe distinctly longer than the second.

SPECIMENS EXAMINED: *Suriname*: ZMA 5918 (4), "Brown's Kreek"; AMNH 76306, RMNH 1849 (2), 1856 (4), 1866 (2), 4641, (plus unnumbered specimens), no specific locality. Saramacca: ZMA (unnumbered), Hendriktop. *Suriname*: CM 50561, Domburg; CM 50499, Onverwacht; AMNH 77455, CM 44251-44252, RMNH (unnumbered), ZMA 5919 (3), Paramaribo; CM 44253-44256, 50586, Powakka.

*Phyllomedusa tomopterna* (Cope)

*Pithecopus tomopternus* Cope, 1868:112.

*Phyllomedusa tomopterna*, Boulenger, 1882:430.

TYPE LOCALITY: "Below mouth of Rio Napo, or Rio Amazonas below mouth of Rio Napo."

DIAGNOSIS: A medium-sized tree frog with vertical pupils, the first toe shorter than the second, and with vertical dark bars on the posterior surfaces of the thighs.

It may be distinguished from *P. bicolor* by its smaller size and the presence of dark bars on the posterior surfaces of the thighs, and from *P. hypochondrialis* by having the first toe distinctly shorter than the second.

SPECIMENS EXAMINED: *Suriname*: RMNH 1856, no specific locality.



*Sphaenorhynchus eurhostus* Rivero

*Hyla aurantiaca* Daudin, 1802:28.

*Sphaenorhynchus aurantiacus*, Myers and Leviton, 1961:61.

*Sphaenorhynchus eurhostus* Rivero, 1969:701 (substitute name).

TYPE LOCALITY: "Brazil."

DIAGNOSIS: A medium-sized, bright-green (white in preservative) tree frog with a very pointed snout, and with a horizontal red or black stripe extending from the tip of the snout to the eye.

The very pointed snout with the dark stripe running horizontally across it from its tip to the eye distinguishes this species markedly from any other small green tree frog of Suriname.

SPECIMENS EXAMINED: *Suriname*: RMNH (unnumbered), "coastal plain"; AMNH 76307, RMNH 1796, no specific locality. *Marowijne*: RMNH (unnumbered), *Wia-wiabank*. *Saramacca*: ZMA (2 unnumbered), *Hendriktop*. *Suriname*: CM 50562, *Domburg*; RMNH 1911 (plus 2 unnumbered), *Paramaribo*.

*Centrolenella fleischmanni* (Boettger)

*Hylella fleischmanni* Boettger, 1893:251-252.

*Centrolella fleischmanni*, Noble, 1924:67.

TYPE LOCALITY: "Costa Rica, San Jose."

DIAGNOSIS: A small centrolenid, with a green or yellowish dorsum in life that fades to a milky white in preservative, that lacks vomerine teeth.

Among the other centrolenids now known from Suriname, *C. fleischmanni* may be distinguished from *C. geijskesi* by the absence of vomerine teeth, and from *C. taylori* in fading to a milky white, rather than lavender, on the dorsum.

SPECIMENS EXAMINED: *Suriname*: RMNH 4463 (holotype of *Hylella cappellei*), no specific locality.

*Centrolenella geijskesi* Goin

*Centrolenella geijskesi* Goin, 1966b:77.

TYPE LOCALITY: "Suriname, District Nickerie, south slope of Wilhelmina Mts., 200 meters altitude."

DIAGNOSIS: A small-to-medium-sized centrolenid with a lavender dorsum (in preservative) and with vomerine teeth.

It may be immediately distinguished, by the presence of vomerine teeth, from all centrolenids now known from the Guianas.

SPECIMENS EXAMINED: *Suriname*: Nickerie: RMNH 11041 (holotype), *Wilhelmina Mts*.

*Centrolenella taylori* Goin

*Centrolenella taylori* Goin, 1968:115.

TYPE LOCALITY: "Guyana, on the New River, at an elevation of 750 feet."

DIAGNOSIS: A centrolenid, without vomerine teeth, lavender on the dorsum after preservation.

It differs from *C. geijskesi* in the absence of vomerine teeth, and from *C. fleischmanni* in being lavender on the dorsum in preservative, rather than fading to a uniform milky white.

SPECIMENS EXAMINED: *Suriname*: Marowijne: RMNH 11474, near Grensgebergte; RMNH 11472, Marowijne R.; RMNH 11473, Nassaugebergte.

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A NEW SPECIES OF *ELEUTHERODACTYLUS*  
(AMPHIBIA, LEPTODACTYLIDAE) FROM HISPANIOLA

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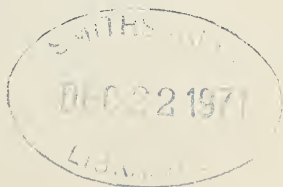
During the summer of 1969, I spent three weeks, with James A. Rodgers, Jr., and James B. Strong, at the headquarters of the Alcoa Exploration Company at Cabo Rojo, Pedernales Province, República Dominicana. While based at Cabo Rojo, we were able to ascend the Sierra de Baoruco along the paved highway that leads to the bauxite mines under operation at Las Mercedes and Aceitillar. The Alcoa road travels from sea level to an elevation of 4400 feet (1342 meters). In this passage, one drives from the xeric coastal lowlands of the Península de Barahona to the pine forests of the higher and well-drained Baoruco uplands. At intermediate elevations there are extensive woods and forests of deciduous trees and *Acacia*. We found that night-collecting along this road was fairly profitable, and early in our stay at Cabo Rojo we secured three specimens of a new species of *Eleutherodactylus* on the paved highway traversing the deciduous woods at intermediate elevations. Several attempts to collect this species in the forest itself proved fruitless, even though localities like the amphitheater-like L'Eglise, with its extensive limestone caves and walls, seemed a likely place for this new species of *Eleutherodactylus*.

Apprised of the finding of the new frog, Robert K. Bobilin and Richard Thomas attempted to secure additional specimens when they spent a week at Cabo Rojo in July and August. Remarkably, they secured none on the highway, but Thomas collected two frogs in a cave at about sea level in the typical xeric situation of the Barahona lowlands. Thus, a total of five specimens of this *Eleutherodactylus* are at hand, from two distinctly different ecological situations.

The present collections were made under the support of National Science Foundation research grant GB-7977, for which I am grateful. Assistance in the field was ably provided by the four men mentioned above. The illustration is the work of Dr. David C. Leber. Our stay at

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Cabo Rojo was made most pleasant through the good offices of Patrick N. Hughson and Miss Ruth Hamor of the Alcoa Exploration Company. In recognition of the hospitality offered us by the staff and administration of the Alcoa Exploration Company at Cabo Rojo, I hereby propose that this new species be called

***Eleutherodactylus alcoae*, new species**

**HOLOTYPE:** CM (Carnegie Museum) 45889, a gravid female, from 22 km. NE Cabo Rojo, 1500 feet (458 meters), Pedernales Province, República Dominicana, taken May 19, 1969 by James A. Rodgers, Jr. Original number ASFS (Albert Schwartz Field Series) V16794.

**PARATYPES:** ASFS V16678, 24 km. NE Cabo Rojo, 2000 feet (610 meters), Pedernales Province, República Dominicana, May 16, 1969, J. A. Rodgers, Jr.; USNM (United States National Museum) 166959, 21 km. NE Cabo Rojo, 1500 feet (458 meters), Pedernales Province, República Dominicana, May 17, 1969, J. B. Strong; MCZ (Museum of Comparative Zoology) 43255, 8 km. N, 2 km. E Cabo Rojo, Pedernales Province, República Dominicana, August 3, 1969, R. Thomas; ASFS V21544, 8 km. N, 2 km. E Cabo Rojo, Pedernales Province, República Dominicana, August 4, 1969, R. Thomas.



Fig. 1. Holotype of *Eleutherodactylus alcoae* (CM 45889), dorsal view; snout-vent length 40.1 mm.

**DIAGNOSIS:** A species of the *ricordi* group of Antillean *Eleutherodactylus* characterized by a combination of moderate size (males to 26 mm., females to 40 mm. snout-vent length), very large digital discs, a dorsal pattern of dark brown marbling or spotting on a yellow-to-tan ground, chin heavily stippled or mottled with dark brown, and generally stocky habitus in comparison with other Hispaniolan members of the group.

**DESCRIPTION OF HOLOTYPE:** A gravid female with the following measurements in millimeters: snout-vent length 40.1, head length 15.7, greatest width of head 16.1, longitudinal diameter of tympanum 3.4, longitudinal diameter of eye 5.2, naris to anterior corner of eye 5.0, femur 17.4, tibia 18.5, fourth toe 14.6, tibia/snout-vent length 46.1. Head slightly broader than distance from snout-to-posterior border of tympanum; snout truncate with nares prominent at anterior ends of canthus rostralis; diameter of eye slightly greater than distance from naris to anterior corner of eye; interorbital space 5.2, equal to diameter of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye equal to about one-third diameter of tympanum. Digital discs present, very well developed, largest on digit three and equal to slightly less than half of tympanum. Fingers relatively long, unwebbed, 3-4-2-1 in order of decreasing length; subarticular tubercles very well developed, very prominent, pale gray. Toes relatively long, all with very slight basal webbing, 4-3-5-2-1 in order of decreasing length; subarticular tubercles large, prominent, and gray. Heels do not touch when femora are held at right angles to body axis. Dorsum smooth to very finely shagreened, with about four or five low rounded warts between angle of jaw, tympanum, and forelimb insertion; throat smooth, venter finely granular with very low granules, belly disc well developed with moderately prominent pectoral and abdominal folds. Dorsal surfaces of all limbs smooth; posterior faces of thighs wrinkled and with low, rounded pavement-like granules. Inguinal and axillary glands present but inconspicuous. Tongue large, ovate, nicked behind, free posteriorly, its greatest width equal to about half that of floor of mouth. Vomerine teeth in two long, arched series from well outside the choanae and adpressed against the posterior margin of the choanae, the two series separated by a distance equal to half the diameter of a choana.

**COLORATION OF HOLOTYPE:** In life, dorsal ground color pale yellow, with all markings grayish brown; concealed surfaces of hindlimbs brown, somewhat marbled with yellow, especially medially. Dorsum completely mottled with grayish brown, without indication of pale dorsolateral longitudinal lines, the mottling in the scapular region forming a widely opened dark chevron; an irregularly edged dark interocular bar with a clear area preceding it, the clear area in turn delimiting the slightly stippled or mottled snout. Upper surfaces of all limbs and digits mottled with grayish brown, digital discs dark brown. Dark loreal bar present but very poorly defined; a dark supratympanic crescent which sends a prominent dark bar ventrally into the center of the tympanum. Venter white, with moderately heavy brown stippling on the lower jaw and throat.

**VARIATION:** The single male *E. alcoae* has the following measurements and ratio: snout-vent length 26.2, head length 10.1, head width 10.9, tympanum 2.7, eye 3.5, naris to eye 3.0, femur 12.4, tibia 13.2, fourth toe 10.5, tibia/snout-vent length 50.4. Four females (including the holotype) have the following measurements and ratios (means enclosed in parentheses): snout-vent length 33.5-40.1 (37.0), head length

13.8-15.7 (14.5), head width 13.6-16.1 (14.6), tympanum 3.0-3.4 (3.2), eye 4.2-5.2 (4.6), naris to eye 4.5-5.0 (4.7), femur 15.2-17.4 (15.9), tibia 15.9-18.5 (17.1), fourth toe 12.7-14.6 (13.7), tibia/snout-vent length 44.5-47.5 (46.2). All but the smallest female are gravid.

The dorsal pattern is as described for the holotype. There is never an indication of pale dorsolateral lines, a pattern feature that distinguishes *alcoae* from *E. pictissimus* Cochran which occurs syntopically (see Schwartz, 1965:103, fig. 89). Color notes taken from the four paratypes (in life) demonstrate the variation in pigmentation:

ASFS V16678 (female). Dorsal ground color yellow-tan, markings dark brown; all upper limb surfaces distinctly yellow, concealed surfaces of hindlimbs brown; hands and feet pale gray; venter white; iris bronzy above and below, black anteriorly and posteriorly, pupillary ring orange.

USNM 166959 (male). Dorsal ground color yellow-green, markings black, concealed surfaces brown.

MCZ 43255 (female). Dorsum (including limbs) pale tan (more or less buff) with brown markings; in sacral region ground color near white and apparently frosted. Concealed surfaces rich (chocolate) brown. Iris appears brown (in artificial light) flecked with gold; pupillary ring gold. Tympanum almost completely circled with heavy chocolate brown ring; short, brown longitudinal mark connects to ring and appears in scapular region as a short dark-edged stripe that fades on the body. Throat whitish, finely stippled with brown to give mottled effect; venter white; under side of legs finely and uniformly stippled brown. Interocular bar brown, buff-edged anteriorly.

ASFS V21544 (female). Coloration like MCZ 43255, but more light flecking on postfemoral surfaces, and with white line below eye. (Color notes from MCZ 43255 and ASFS V21544 taken by Richard Thomas, all other by Schwartz.)

COMPARISONS: Two other species of *Eleutherodactylus* on the Hispaniolan south island (*sensu* Williams, 1961) might be confused with *E. alcoae*: *E. pictissimus* Cochran and *E. counouspeus* Schwartz. Neither has been heretofore collected on the southern slope of the Sierra de Baoruco where *E. alcoae* occurs, but during the summer of 1969, five *E. p. pictissimus* were taken in this region at the following localities (all in Pedernales Province): ASFS V16753, 22 km. NE Cabo Rojo, 1700 feet (519 meters); ASFS V16759, 21 km. NE Cabo Rojo, 1300 feet (397 meters); ASFS V16802, 21 km. NE Cabo Rojo, L'Eglise, 1300 feet (397 meters); ASFS V21472-73, 26 km. N Pedernales. The nearest previously recorded locality for *E. p. pictissimus* is Thiotte, Dépt. de l'Ouest, Haiti, across the Dominico-Haitian border on the southern slope of the Massif de la Selle (Schwartz, 1965:107). Another subspecies (*E. p. apantheatous* Schwartz) occurs along the eastern margin of the Península de Barahona and along the northern slope of the Sierra de Baoruco. Both *E. alcoae* and *E. pictissimus* thus occur syntopically at least north of Cabo Rojo



(and presumably elsewhere). The two species are easily distinguished both by pattern and morphology, although their basic hues and pattern elements are remarkably similar. *E. alcoae* always lacks pale dorsolateral lines, a feature that *E. p. pictissimus* always demonstrates. *E. alcoae* has very large digital discs, whereas *E. pictissimus* has the discs very feebly developed. The two species are comparable in size. The largest female *E. p. pictissimus* examined (of 53 specimens from Haiti and the República Dominicana) has a snout-vent length of 42.1 mm. and is from 21 km. NE Cabo Rojo (and thus within one kilometer of the type locality of *E. alcoae*). The largest male *E. p. pictissimus* examined (of 40 from Haiti and the República Dominicana) has a snout-vent length of 33.9 mm. and is from the vicinity of Jérémie, far to the west near the tip of the Tiburon Peninsula in Haiti. As far as present data indicate, *E. p. pictissimus* reaches a larger size than *E. alcoae*, but the very limited material of the latter species precludes detailed comparison. The more stocky habitus of *E. alcoae* is obvious to the eye, but ratios of tibia to snout-vent length in female *E. alcoae* (44.5-47.5) are included within the limits of this ratio in female *E. p. pictissimus* (42.0-53.3), and the same is true for the ratio of the single *E. alcoae* (50.4) in reference to those of male *E. p. pictissimus* (41.3-53.2). Aside from the chromatic, pattern, and size characteristics that separate *E. alcoae* from *E. p. pictissimus*, the two species are also easily differentiated by the presence of dark lower-jaw and throat stippling and clouding in *E. alcoae* in contrast to the very light throat stippling in *E. p. pictissimus*.

*E. counouspeus* has been known only from the holotype, taken at Grotte de Counou Bois, Dépt. du Sud, Haiti, on the westernmost portion of the south versant of the Massif de la Hotte, far to the west of the known range of *E. alcoae* (Schwartz, 1964). Since that time, a long series of *E. counouspeus* has been collected at Grotte de Forêt, ca. 9 km. (air-line) WSW Jérémie, Dépt. du Sud, Haiti, by Richard Thomas, and more recently a single individual was secured by T. Preston Webster and A. R. Kiester at a locality 1.5 mi. (2.4 km.) S. Castillon, 2500 feet (763 meters), Dépt. du Sud, Haiti. Thus *E. counouspeus* seems to be widely distributed over the extreme tip of the Tiburon Peninsula in the Monts Cartaches and on both slopes of the Massif de la Hotte, all in Haiti and well to the west of the known stations for *E. alcoae*.

*E. counouspeus* reaches a much larger size than does *E. alcoae*. Adult female *E. counouspeus* have snout-vent lengths of 57.1 mm., adult males to 48.0 mm. The two species are somewhat comparable in pattern, al-

though the markings are more marked in *counouspeus* than in *alcoae*. The ground color in *E. counouspeus* is olive-green to greenish-yellow, and males have the throat olive, spotted, or marbled with yellow. The presence of a vocal sac in male *E. counouspeus* also differentiates that species from *E. alcoae*. In fact, despite the superficial similarity between these two species, they belong to two different sections of the genus, and similarity of ground color and pattern probably is due to convergence because of similar habitats. It seems likely that *E. alcoae* is a southern Baoruco versant derivative of *E. pictissimus*.

REMARKS: As stated in the introduction, the three specimens taken by Rodgers, Strong, and myself were all collected from the paved Alcoa highway between elevations of 1500 and 2000 feet (458 to 610 meters). At this intermediate elevation, the Sierra de Baoruco is heavily forested with deciduous trees and interspersed *Acacia*, all on a limestone foundation. At the time of our visit, these slopes were luxuriantly green, since daily rains were falling on the southern versant. *E. alcoae* was rarely encountered on the highway in this region, despite many hours of night-collecting along the road. A nocturnal visit to L'Eglise, a much eroded limestone amphitheater at 1300 feet (397 meters), after a heavy afternoon rain, yielded no specimens of *E. alcoae*, and indeed very few of any species of *Eleutherodactylus*. Richard Thomas secured two specimens of *E. alcoae* on two visits to a cave on the Oviedo-to-Pedernales road. The first frog was taken in the cave near a small pool of water beyond the twilight zone and in nearly full darkness. The cave has several isolated pools, including the one beyond which the frog was caught and which was quite deep (between six and eight feet). The floor of the cave had scattered landcrab burrows in which standing water also was visible. The second frog was collected in a similar situation.

The cave is located in xeric *Acacia*-cactus scrub in what is otherwise an extremely hostile habitat for most amphibians. Questioning residents of Cabo Rojo, I was advised that no frogs occurred in that region. However, after heavy lowland rains, we collected *Hyla dominicensis* Tschudi, and heard small choruses of this species in scattered temporary pools between Cabo Rojo and the intersection of the Alcoa road with the Oviedo-Pedernales road, and both east and west along the latter. The cave where the two *E. alcoae* were taken lies at the very southern margin of the Sierra de Baoruco where the latter begins its ascent from the arid plains that form the Península de Barahona. Presumably *E. alcoae* has a wider latitudinal distribution than now known. It seems likely that it

occurs also in Haiti to the west along the southern slopes of the Massif de la Selle, and further east in the República Dominicana along the southern slope of the Sierra de Baoruco. Its altitudinal distribution in this area may well be limited by the occurrence of pine woods above the belt of deciduous trees wherein *E. alcae* occurs. These higher-elevation pine woods are quite sterile as far as *Eleutherodactylus* is concerned, and we collected only *E. abbotti* Cochran in this situation near Aceitillar.

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A SMALL SKULL OF THE LOWER PERMIAN  
REPTILE *DIADECTES* FROM THE WASHINGTON FORMATION,  
DUNKARD GROUP, WEST VIRGINIA

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INTRODUCTION

The presence of the primitive reptile *Diadectes* throughout much of the content of the lower Permian terrestrial deposits of the western United States has long been well established on the basis of a great number of specimens, including many that are excellently preserved. Only recently has the existence of *Diadectes* in beds of this age in the northeastern United States been firmly established. Olson (1970) has reported *Diadectes* from the Washington formation, Dunkard group, in Ohio, and although his identification was based on fragments of vertebrae (personal communication), they definitely pertain to this genus. Two other diadectid specimens, closely related to *Diadectes*, have been reported from the upper Pennsylvanian, Conemaugh group, near Pittsburgh, Pennsylvania. These have been described by Romer (1952). Identification of one of these, *Desmatodon hollandi*, was founded on a fragment of maxillary with four teeth and the root of a fifth. The other specimen is a small left dentary (11 mm. in length), possessing eight teeth of a diadectid character that are seemingly more primitive than those of *Desmatodon hollandi*. Romer provisionally referred it to *Desmatodon*, suggesting that it may pertain to an immature individual with some sort of "milk dentition." Finally, Langston (1963) reported the presence of diadectids from the Permian beds of Prince Edward Island. A fragment of a left dentary, containing roots of six teeth in a length of 10.5 mm., was too incomplete to permit certain generic assignment and was referred to Diadectomorpha. Langston discovered, however, a postzygapophysis of a dorsal vertebra that could safely be referred to *Diadectes*.

To date, all reports of diadectids from the eastern United States and

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Prince Edward Island have been based on fragments, either of vertebrae or of jaws. Though admittedly some of these remains are indistinguishable from the well-known specimens of *Diadectes* from the western United States, there has been no assurance that this similarity would extend to their total osteology. The *Diadectes* skull described below from the lower Permian Washington formation of West Virginia would seem to reinforce the assumption that these spatially wide-ranging specimens of *Diadectes* are indeed alike.

The assignment of the diadectids to the cotylosaurian reptiles has recently been questioned by Romer (1964), who has argued for their placement among the advanced anthracosaurian labyrinthodont amphibians. The diadectids, however, display a number of skeletal features that are clearly reptilian. Until this controversy can be resolved with knowledge of their mode of development, it seems best to retain the more widely accepted view that they had attained a reptilian structural grade.

The events leading to my opportunity to describe the specimen that prompted this paper were fortuitous. The specimen was found in April, 1970, by Jeffrey Sommerville, 10, and Jimmy Stewart, 12, both residents of Reedy, Roane County, West Virginia. The site of their discovery was along the bank of Reedy Creek about a half mile south of the town of Reedy and just west of State Route 14. The fossil had obviously been transported by the creek some distance from its original site of deposition. It was eventually brought to Miss Sandra Elmore, an instructor at nearby Spencer High School, who, thanks to her knowledge of the local geology and her interest in paleontology, recognized the possible importance of this find and brought it to Carnegie Museum. I am indebted to each of these persons for the opportunity to study this specimen, a cast of which has been incorporated in the vertebrate fossil collections of Carnegie Museum as CM 24127. The actual specimen is temporarily in the custody of Carnegie Museum, pending resolution of the question of ownership between the finders and the landowner on whose property it was found. Thanks also are due to Herbert Klug for the preparation of the latex casts seen in figure 3, and to Hinda Barsky for typing the manuscript. Field trips to West Virginia for purposes of geological reconnaissance were made possible through a grant from the Gulf Oil Corporation. Throughout the text that follows, the skull and casts alike are referred to as CM 24127, although in fact the skull itself is not included under that catalogue number.



## SYSTEMATICS

## Class Reptilia

## Subclass Anapsida

## Family Diadectidae

*Diadectes* sp.

## Figures 1, 2

**HORIZON AND LOCALITY:** The *Diadectes* skull, CM 24127, was found lying on the muddy bank of Reedy Creek a half mile south of the town of Reedy and just west of State Route 14 in Roane County, West Virginia. The only sediments exposed in this region are of the Washington formation, Dunkard group, lower Permian. The skull had undoubtedly been transported by Reedy Creek at least some distance from its original site of deposition and the only clue to its precise stratigraphic origin is the sandstone of which it is composed. This assumes, however, that the sandstone of the specimen, which represents a filling of the original bony skull and mandibles, is identical with sediments from which it was eroded free. A stratigraphic section, measuring 139 feet in thickness and well within the Washington formation, described by Hennen (1911: 139), begins at the north end of the town of Reedy and continues southeast to Reedy Creek. The upper portion of this section includes in descending order: 22.5 feet of the upper Marietta sandstone; 52.5 feet of the red Creston shale; 16 feet of sandstone and limy shale, mostly shale; and 5 feet of the lower Marietta sandstone. The sandstone of CM 24127 is identical to that of the upper and lower Marietta sandstones. Of the two sandstone units, only outcrops of the lower Marietta sandstone occur close to where the specimen was found. Exposures of this sandstone are seen in a road cut on the east side of State Route 14, opposite the place where the skull was found. It seems reasonable, therefore, to suspect that CM 24127 was derived from the lower Marietta sandstone of the Washington formation.

**DESCRIPTION AND DISCUSSION:** The *Diadectes* skull, CM 24127, from West Virginia is an internal mold of the skull and mandibles, consisting of a medium-grained, slightly micaceous sandstone. All bones that surrounded or penetrated the sandstone matrix filling of the skull and jaws have weathered away completely, but imprints of some of the sutures are visible. The total absence of bone in this specimen is probably the result of dissolution by ground water prior to areal exposure. Despite the unusual nature of preservation, this internal mold faithfully repro-

duces the gross features of skull and lower jaw, all of which conform very closely to those present in the family Diadectidae. Those diadectid features that are visible on CM 24127 (figs. 1, 2 and 3) and that are listed by Romer (1956: 486) as characteristic of this family are described as follows: "Skull short, high, with a broadly rounded muzzle . . . Jaw articulation a short distance in advance of level of condyle; otic notch deep dorsoventrally, with concave anterior border; articulation well below level of tooth row, the cheek deep.

" . . . Palatine, in addition to forming portion of palatal roof, develops a medial shelf at a lower level, internal to tooth battery of cheek . . . Quadrate large, vertically placed, broad mediolaterally, concave posteriorly in lateral view, its upper end hooked backward to gain contact with the tip of the paroccipital and associated dermal elements . . .

"Jaw short and deep, upper margin rising posteriorly to coronoid region and descending steeply to articular region, which is placed far below level of tooth row. Medial jaw fenestra large . . . Marginal dentition of chisel-like 'incisors' and a battery of eight to twelve transversely expanded cheek teeth with a central cusp and lateral and medial 'shoulders' . . ." The assignment of CM 24127 to the family Diadectidae is unquestionable.

Generic assignment of CM 24127 poses only minor uncertainties. Romer (1956 and 1966) lists three North American genera belonging to this family: *Desmatodon* (late Pennsylvanian), and *Diadectes* and *Diasparactus* (early Permian). Impressions of the teeth on the specimen reveal a dentition (discussed below) of the more advanced type found only in the latter two genera, thus eliminating the possibility that the skull pertains to the more primitive *Desmatodon*. Conservative judgment rules in favor of assignment of the skull to *Diadectes* rather than to *Diasparactus*. There is but one known species of *Diasparactus*, *D. zenos*, which is based on two specimens (see Case and Williston, 1913) from the early Permian beds of northern New Mexico. One of these specimens is a nearly entire skeleton. Although imperfectly preserved, the skull, except for some minor differences, agrees very closely with *Diadectes*. Most of the apparent differences of *Diasparactus zenos* from other diadectids are seen in its more completely known postcranial skeleton, particularly the vertebrae. Because specimens of *Diasparactus* are extremely rare and have a very limited geographic range, it seems advisable to refer the West Virginia diadectid skull described here to *Diadectes*, which is known from a great number of specimens found

over a very extensive region that includes in the western United States parts of Arizona, Colorado, New Mexico, Oklahoma, Texas, and Utah.

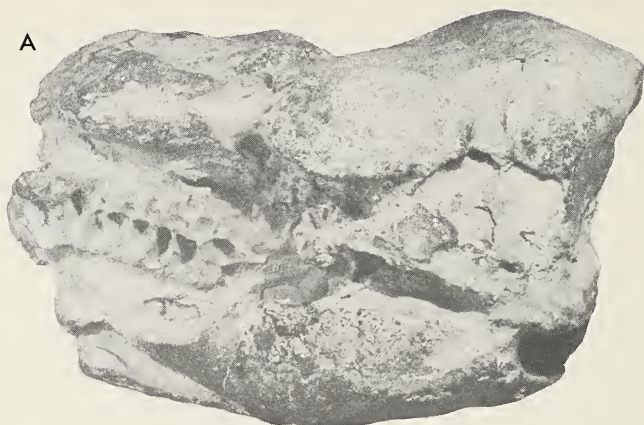
The *Diadectes* skull from West Virginia is relatively small. It is about two-thirds the size of the skull illustrated by Olson (1947), which is a composite based on the lower Permian species *D. sideropelicus* from the Wichita group, and *D. tennuitectes* from the Clear Fork group of Texas. The restoration given by Case and Williston (1912) of a skull of *Diadectes lentus* from the early Permian of northern New Mexico is about twenty to thirty per cent longer. Lewis and Vaughn (1965) have described what they believe to be an immature specimen of *Diadectes*, *D. sanmiguelensis*, from the early Permian of Colorado, which is about two-thirds as large as CM 24127. There is no compelling evidence to suggest, however, that the West Virginian specimen is immature.

Most of the major structural features that can be gleaned from CM 24127 are indicated in figures 1, 2 and 3, and only the dentition requires comment. There has been little or no distortion of the skull. Even the lower jaws are in their proper orientation, so that the resting occlusal position between the upper and lower dentitions appears to have been quite accurately preserved. A small portion of the anterior tip of the snout was lost, and posteriorly the occiput of the skull is not represented. The length of the skull, measured along the dorsal midline from the tip of the snout to the posterior edge of the parietal—about 5.0 mm. behind the parietal opening—is about 105.0 mm. To this must be added a few millimeters to account for the loss of the tip end of the snout and the loss of the skull roofing bones.

Each mandible is represented predominantly by the endocast of its large internal canal. Portions of the sutural patterns, in some places well defined, can be seen on the upper and lower jaws. Unfortunately, sutures cannot be determined for the remainder of the dermal roofing bones of the skull. These have been lost either through weathering or by the fusion of adjacent bones with age. According to Olson (1950: 63), in the *Diadectes* specimens he studied, "Fusion of adjacent elements in the occipital and temporal regions appears to have been initiated at an early stage and to have progressed from the inner to the outer surface of the skull." Latex casts of both sides of CM 24127 reveal a small portion of the palatal process (fig. 3C) of the palatine bone, an outstanding feature of the palate of this genus. Olson (1947) believes that these processes represent a partially developed secondary palate that may have been completed by membrane. Noteworthy here also, is a narrow,

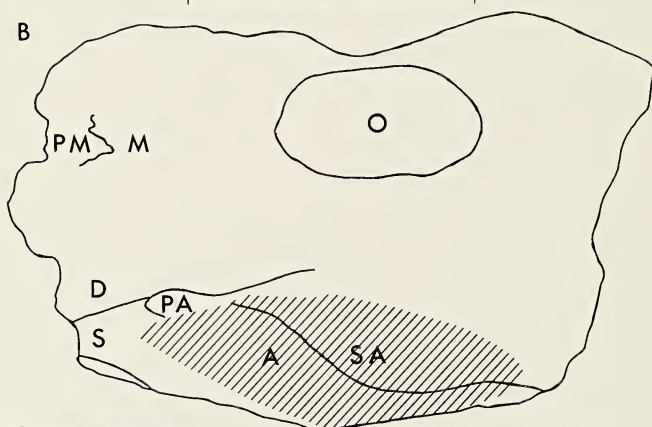


A

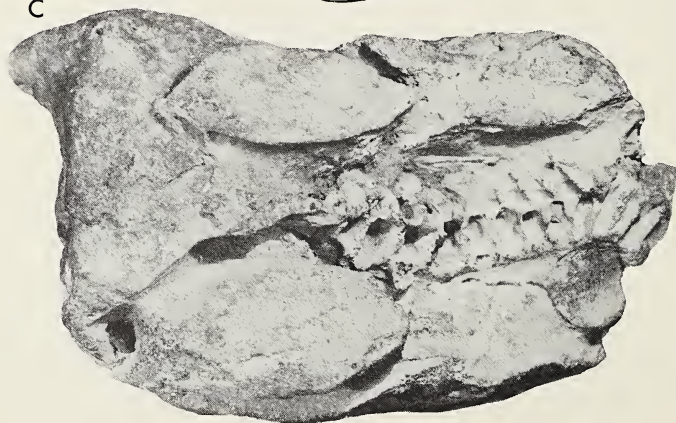


5 cm.

B



C



shallow groove that is visible on both the right and left maxillaries. As indicated in fig. 3C, it can be traced posteriorly and dorsally onto the dorsal surface of the maxillary, where it ends at a level above the eleventh tooth. Vaughn (1969) reports finding the same channel in *Desmatodon hesperis* and in various specimens of *Diadectes*. Its function has not yet been determined.

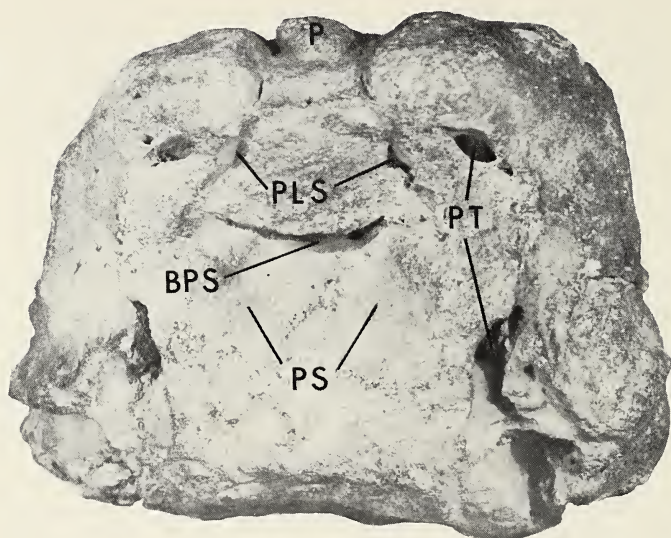
As mentioned above, none of the occipital bones are represented. The posterior face of the specimen (fig. 2A) is actually a view of the braincase exposed in transverse section. This section is nearly vertical, passing downward from the level of the posterior border of the parietal, directly behind the pineal opening, and through the braincase at about the level of the sella turcica. Impressions of the uniquely diadectid parasphenoidal wings are visible on the posterior face of the specimen. In *Diadectes* the parasphenoid divides posteriorly into two broad wings, which underlie the basioccipital and the paroccipital processes of the opisthotic (Olson, 1947). The opening immediately above the parasphenoid impression was occupied by the fused parasphenoid and basisphenoid bones. The plug of matrix above this opening and between the paired openings for the ?pleurosphenoid bones represents the braincase cavity. Two pairs of openings that held the quadrate rami of the pterygoids are also clearly seen.

Most of the teeth of the upper and lower jaws on both sides of CM 24127 are preserved, but as impressions, or more precisely, as partial molds only. Fortunately, however, the latex casts of these molds shown in figure 3 render an accurate and nearly complete restoration of the upper and lower dentitions as they would have appeared in medial view. Nowhere do these casts include any portion of the lateral aspect of any of the teeth. This is due to the absence of the lateral walls of the mold-like impressions of the teeth. In all, nine maxillary and 13 dentary teeth can be readily seen on the left side of the skull (figs. 1A and 3A), while on the right side (figs. 1C, 3B and C) the dental series are more completely represented, consisting of at least 10 maxillary and 14 dentary teeth. None of the premaxillary teeth are clearly indicated on either side of the skull. Despite imperfect preservation, it can be said



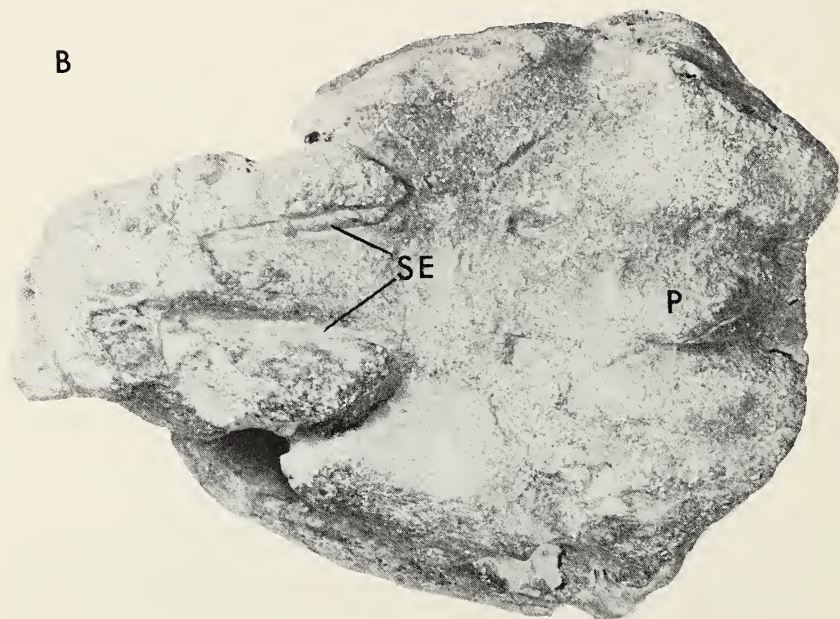
Fig. 1. *Diadectes* sp., CM 24127. A. left lateral view; C. right lateral view. B. outline sketch of A., indicating the preserved limits of the orbit (O), the endocast of the lower jaw canal (oblique ruling), and the traceable sutures demarking portions of the angular (A), dentary (D), maxillary (M), prearticular (PA), premaxillary (PM), surangular (SA), and the splenial (S) bones.

A



5 cm.

B





with reasonable certainty that the dentition of CM 24127 does not differ in any important way from that described for other species of *Diadectes*.

Although the impressions of the premaxillary teeth on either side of the specimen have been lost through weathering, it is quite likely that there were four procumbent "incisors," the normal pattern for *Diadectes* (see Olson, 1947, fig. 1, and Romer, 1956, fig. 43A). The remainder of the marginal dentition in both the upper and lower jaws is best preserved on the right side of the skull. The description given below of the general features of the dentition of CM 24127 is a composite picture, based for the most part on the latex cast in figure 3B, which shows in medial view the dental series of the right upper and lower jaws.

The maxillary held a series of at least 10 and possibly 11 teeth, bringing the probable minimum number of teeth in the upper jaw to 14 or 15. A check of the literature indicates that the number of maxillary teeth in *Diadectes* varies from 11 to 13. The maxillary teeth in CM 24127 increase in size posteriorly to about the eleventh or twelfth tooth of the upper jaw. Posterior to this the teeth are abruptly smaller. The first two teeth of the maxillary are slightly procumbent. The tenth tooth of the right upper jaw is newly erupted and had not fully moved down into permanent position. Circular pits are present along the lingual sides of the bases of many of the maxillary teeth. These pits are of the type generally found in *Diadectes* (Welles, 1941) and *Desmatodon* (Vaughn, 1969). They are referred to as "basal notches" by Welles, who describes their role (p. 428) as follows: "When replacement is about to occur, the lingual base of the tooth is resorbed and a notch is developed . . . Beneath this notch lies the crown of the succeeding tooth, ready to replace the original . . ."

The entire dentition of the right lower jaw, except for the possible absence of the last one or two teeth, is represented by an unbroken series of 14 teeth. This is in agreement with the condition in *Diadectes lentus*, in which, according to Welles (1941), the number of teeth in the lower jaw varies from 14 to 18. The differentiation of the teeth in CM 24127 is

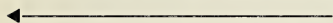
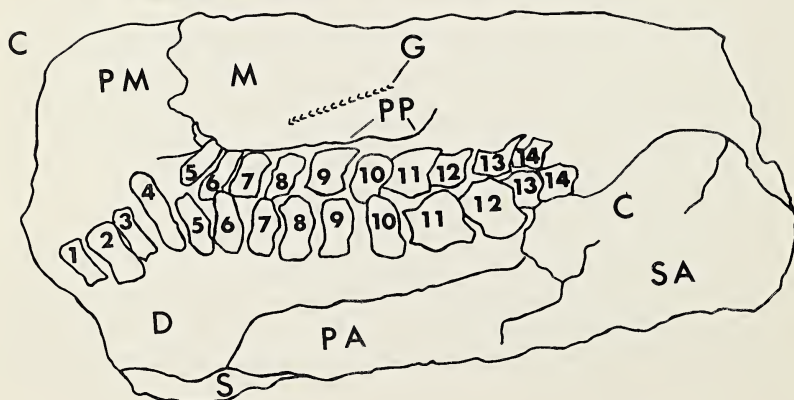


Fig. 2. *Diadectes* sp., CM 24127. A. occipital view; B. dorsal view. The fused basiparasphenoid (BPS), the probable pleurosphenoids (PLS), and the quadrate rami of the pterygoids (PT) are seen as openings in the skull. The posterior wings of the parasphenoid (PS) and the areas of attachment of the sphenethmoids (SE) to the skull roof are represented by impressions. The pineal opening is indicated by a well-defined prominence (P).



5 cm.



also in close accord with that seen in *Diadectes*. The first four teeth are obviously procumbent "incisors" of nearly equal height. Their bases exhibit the longitudinal striae characteristically seen in diadectids. The fourth right incisor in figure 3B best illustrates the diadectid features of these teeth. The upper half of the lingual face of the tooth is beveled, giving the tooth a chisel-like form. There is a shallow groove on the beveled surface caused by wear. Posterior to the first four incisors on the right lower jaw there begins immediately an uninterrupted series of 10 cheek teeth. The first of these is only about half the height of the incisors and is intermediate in form between the anterior incisors and the more posterior cheek teeth. Posteriorly, the cheek teeth gradually become larger, more molariform and transversely expanded in the same manner as seen in other specimens of *Diadectes*. The last two teeth of the series are abruptly smaller. Well-defined lingual notches are also seen alongside many of the teeth of the lower jaws.

The tenth upper and lower opposing, molar-like cheek teeth on the right side are newly erupted and their lack of wear allows some comparison with the cusp pattern in *Diadectes*. Although the latex cast in figure 3B lacks the lateral cusps of these two teeth, the central and medial cusps are well preserved, and they exhibit the same reversed pattern of orientation and development that has been pointed out by Romer (1952: 86) as occurring in *Diadectes*. On the right upper tenth tooth the principal central cusp is positioned lateral to the center of the crown, while in the opposing lower tooth the central cusp is displaced to the medial side of the center of the crown. Further, the medial cusp on the upper tooth is more strongly developed than the medial cusp on the lower tooth. The contrary condition would have been expected in the lateral cusps. The eleventh and twelfth pairs of opposing cheek teeth on the right side of CM 24127 are in advanced stages of wear and clearly demonstrate the peculiar reversed pattern of wear in *Diadectes* cheek teeth. Wear of the teeth produces flat surfaces on the lingual side of the



Fig. 3. Latex casts made from A., left side, and B., right side of *Diadectes* sp., CM 24127, showing in medial view the upper and lower jaws and their dentitions. C. outline sketch of B., indicating the preserved teeth and their serial position, and those traceable sutures demarking portions of the coronoid (C), dentary (D), maxillary (M), prearticular (PA), premaxillary (PM), splenial (S), and the surangular (SA). Also shown is the channel (G) on the maxillary and the palatal process (PP) of the palatine bone.



upper teeth, while the same effect is produced on the labial side of the lower teeth.

The state of preservation of the dentition places severe limitations on the measurements that can be made on the cheek teeth. Only those of the right lower jaw are sufficiently preserved for adequate measurements. The largest of these, the tenth, eleventh, and twelfth teeth, have a maximum height of about 9.0 mm., measured from the lingual border of tooth alveolus; a mediolateral width of about 10.3 mm., measured through their transverse axis; and an anteroposterior width of about 4.0 mm., measured through the crown. In both the upper and lower jaws the transverse axis of the cheek teeth is not quite perpendicular to the long axis of the jaw, but is oriented so that the medial end of the tooth is slightly more posterior than the lateral end. This is as would be expected in *Diadectes*.

Dentition affords the best, and possibly the only, means of distinguishing CM 24127 from the closely related upper Pennsylvanian genus, *Desmatodon*. Only two species of this genus are known: *D. hollandi* and *D. hesperis*. *Desmatodon hollandi* was described by Case in 1908 from a fragment of left maxillary, with four teeth and the root of a fifth, discovered at Pitcairn, Pennsylvania (Conemaugh group). This specimen was restudied by Romer (1952) and more recently by Vaughn (1969). Vaughn has shown that the teeth in the holotype of *Desmatodon hollandi* probably include the fifth through the eighth maxillary teeth and the root of the ninth. This series, therefore, most likely includes those cheek teeth with the greatest degree of "molarization." Romer (1952: 86) contrasted the upper cheek of *Desmatodon hollandi* with *Diadectes* as follows: "In *Diadectes* the inner portion of an upper tooth is greatly expanded, and a secondary cusp is there developed, between which and the primary [central] cusp a wearing surface arises . . . In *Desmatodon* the secondary cusp is not present as such, but there is a highly developed medial swelling . . . and in two of the four teeth there is here a small area of wear. In *Diadectes* upper 'molars' there is also present a tertiary lateral cusp and a smaller, secondary area of wear between it and the principal cusp. In *Desmatodon* this region is somewhat developed although lacking a formed cusp, and one of the four teeth shows wear here. The *Desmatodon* teeth thus appear to be built on the fundamental *Diadectes* pattern, but are far more archaic than in *Diadectes*; the most highly developed *Desmatodon* teeth are comparable to the least developed molars of *Diadectes*—those at the front or back

ends of the 'molar' batteries." The well-developed medial cusps on the cheek teeth in CM 24127 clearly justify its assignment to *Diadectes*.

Our knowledge of *Desmatodon* has recently been greatly expanded by Vaughn (1969), who has described a second species of this genus, *D. hesperis*, from upper Pennsylvanian (Missourian age) deposits of the Sangre de Cristo formation of central Colorado. The holotype is based on a nearly entire left maxillary bone, with a complete dentition of 12 teeth. "The difference in general aspect between the dentitions of the two species [of *Desmatodon*]," Vaughn notes (p. 16), "might be summed up by saying that the teeth in *D. hesperis* tend more toward an overall conical shape, and presumably this is more primitive than the condition in *D. hollandi*." Accordingly, there is little likelihood of confusing the dentition of CM 24127 with that of *Desmatodon hesperis*.

#### CONCLUDING REMARKS

Early Permian and late Pennsylvanian fossils from the northeastern United States have come predominantly from pond or lake deposits and are of the type that reflect this sort of standing-water habitat. Recently, however, Olson (1970) has listed a number of newly discovered animals from the lower Permian Washington formation, which he believes point to a truly terrestrial component in the faunas of this region. These have come, for the most part, from deposits of a terrestrial aspect and include a labyrinthodont amphibian, *Trematops stonei*, found in the Creston shale at Marietta, Ohio, and the reptiles, *Dimetrodon* and *Diadectes*, found in a channel-fill directly above the upper Marietta sandstone 10 miles southwest of Marietta near Belpre, Ohio.

With regard to Olson's observations, it is noteworthy that the *Diadectes* specimen from West Virginia was found relatively close to the above localities—about 35 and 28 miles southeast of Marietta and Belpre respectively—and from almost the identical stratigraphic level. Of primary significance, however, is its discovery in a lithology, the lower Marietta sandstone, that is also suggestive of terrestrial rather than pond-lake habitat.

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THE MAMMALIAN FAUNA OF THE LOST CABIN MEMBER,  
WIND RIVER FORMATION (LOWER EOCENE) OF WYOMINGDANIEL A. GUTHRIE<sup>1</sup>

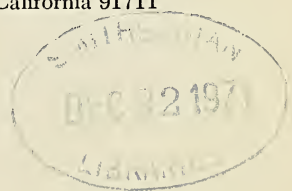
## INTRODUCTION

Although the Lost Cabin is one of the standard subdivisions of the North American early Eocene, the Lost Cabin type fauna, last reviewed by Matthew (1915a, b, c, 1918) and Granger (1915) in their revision of Wasatchian faunas, has never been completely described. This paper revises the Lost Cabin fauna, presenting measurements and figures of each species for which such information has been unavailable. It is hoped that this treatment will facilitate both future comparisons of the Lost Cabin fauna with other early Eocene faunas, and studies of the groups included within the fauna.

## HISTORY OF INVESTIGATION

Fossils were first discovered in Lost Cabin deposits in the Wind River Basin by Jacob L. Wortman, collecting for Cope in 1880 (see Cope, 1881). Although Wortman also made small collections for the American Museum of Natural History in 1891 and 1896, the Lost Cabin deposits were not thoroughly prospected until 1909, when Walter Granger made extensive collections for the American Museum. According to Granger's notes and specimen labels, this latter collection and smaller ones made in 1905 and 1910 came almost entirely from three localities. A fourth area also yielded some remains. The richest area, located about five miles northwest of the town of Arminto on the Sullivan Ranch (sec. 6, T.37N., R.87W.), Natrona County, Wyoming (Davis Ranch on American Museum labels), is referred to here as Locality 1 (see fig. 1). The two other productive areas are located in sec. 22, T.38N., R.89W., Natrona County (Buck Spring on American Museum labels, locality 3 here), and in sec. 22, T.37N., R.88W., Natrona County (Wolton on American Museum labels, locality 2 here). Granger also found a few fossils along Muddy Creek, in the western part of the Wind River Basin.

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Wortman's early collections, which lack precise locality data, undoubtedly came from these three most productive areas.

More recent collecting efforts in the Lost Cabin were those of Princeton University in 1928 and 1931 at locality 1; Amherst College in 1948 and 1957 at locality 3 ('type locality' in Amherst field notes); U.S. Geological Survey under Ted White in 1947 and 1948, around Boysen Reservoir near the Muddy Creek area (White, 1952); Henry Seton in 1929, and Seton and Horace E. Wood II in 1931, near Muddy Creek; and Craig Black for Carnegie Museum in 1968 at locality 1. I have collected at all these localities from 1965-1969, and at a new locality a mile west of locality 3 (sec. 21, T.38N., R.89W., Natrona County, Wyoming, locality 4). My collection is now in the Carnegie Museum. All the above collections have been examined and are included in this review.

#### ACKNOWLEDGEMENTS

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#### METHODOLOGY

Measured samples of lower dentitions are presented wherever possible. Measurements were made with dial calipers, the dial calibrated to 0.1 mm.

The following abbreviations are used, in addition to those noted in the acknowledgements: a, approximate measurement; M, mean; N, num-

ber; OR, observed range; s, standard deviation; V, coefficient of variation.

### GEOLOGY

When the Wind River formation was first explored, it was thought to contain a single fauna, characterized by the presence of *Lambdotherium*. Later, when the Lysite fauna was discovered, the term Lost Cabin

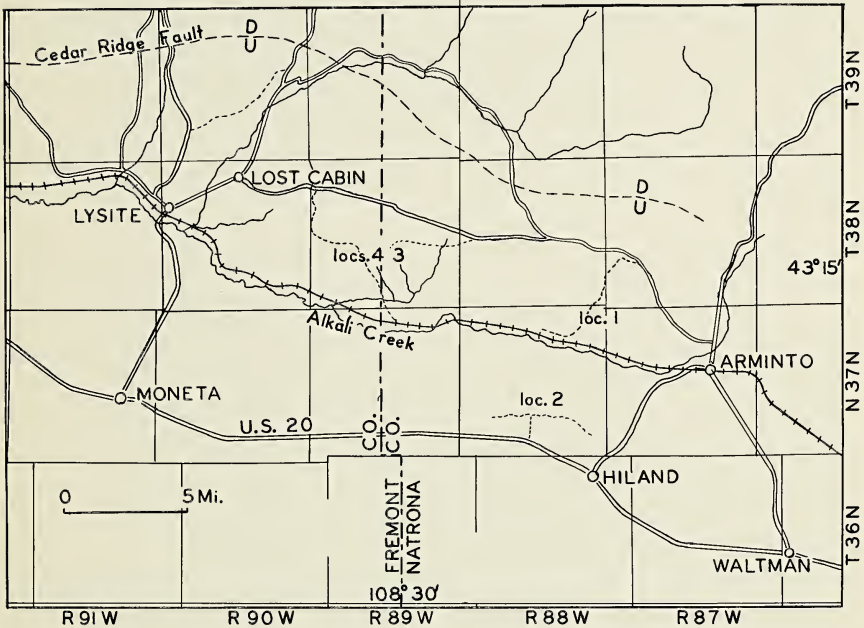


Fig. 1. Sketch map of type area of the Lost Cabin Member, Wind River formation, of Wyoming, showing the locations of the major vertebrate fossil localities. Base taken from Arminto Quad, NK 13-1, 1: 250,000 series, U.S. Dept. of the Interior, Geol. Surv.

was given to the younger sediments within the Wind River formation that contained *Lambdotherium* (Granger, 1910; Sinclair and Granger, 1911). Since that time, the geology of the Lost Cabin member of the Wind River formation has been well described by several authors, notably Tourtelot (1946, 1953), Tourtelot and Thompson (1948), and Keefer (1965). The term Lost Cabin has come to be associated in a broad sense with any fauna containing *Lambdotherium*, and is the basis for the Lostcabinian substage of the early Eocene (see Gazin, 1962: 5). However, material collected from the Lost Cabin member is almost

exclusively from a narrow section at the base of these deposits.

Locality 1, the source of the major portion of the Lost Cabin collections, is characterized by a maroon shale layer about 10 feet thick. The base of this layer is hard, forming shelves in the badlands. It is from these shelves that most fossils have been recovered. This maroon shale also appears at localities 2 and 3, and here again is the source of most of the fossils. To the west of locality 3 this maroon shale layer disappears, to be replaced by a dark-gray shale layer, again forming shelves in the badlands, and the source of most specimens from locality 4. Nearly all material from these localities was collected in a vertical interval of no more than 40 feet. Since this material includes over 95 per cent of all Lost Cabin fossils recovered, the entire collection can be considered isochronous.

The term Lost Cabin, as used in this paper, refers only to the fauna recovered from localities 1-4, representing a very narrow time zone and section within the Lost Cabin member of the Wind River formation. This zone is included in, but does not coincide with, the Lostcabinian period (= *Lambdotherium* zone). *Lambdotherium* has been recovered from the upper portion of the Lysite member of the Wind River formation (Guthrie, 1967a) and may not be present in the upper portion of the Lost Cabin member of the Wind River formation, which may be middle Eocene in age. Only one faunal level is known in the Wind River Lost Cabin deposits. Osborn (1909) described two levels, an earlier one with *Lambdotherium* and without *Eotitanops*, and a later one with both genera present. This view, caused by a misinterpretation of field notes, was corrected by Granger (1910: 241) and by Osborn (1929: 279, fig. 4) but reappears in Robinson (1966; ascribed to Osborn 1929 but probably 1909). Localities on Muddy Creek and in the Boysen Reservoir area have not been correlated with the maroon shale layer of locality 1, but seem to have an identical fauna.

Collections from localities 1, 2, and 3 do not differ significantly in content. Locality 4, however, differs in both preservation and content from the other localities. Only isolated teeth have been recovered at locality 4, mostly from a very narrow shale layer in association with copious gar and crocodile material. These specimens are abraded and appear stream-worn. The fauna is more aquatic in nature than that of localities 1, 2, and 3, and contains more *Coryphodon* and perissodactyl material.



## THE FAUNA

### COMPOSITION

The Wind River Lost Cabin fauna contains 77 species belonging to 53 genera and 13 orders (table 1). The minimum number of individuals for each species is the minimum number of individuals necessary to account for the specimens recovered, calculated separately for each locality. The numbers for each species presented here disagree with those of Osborn (1929). His larger estimates of numbers for all species, especially *Lambdotherium*, *Hyracotherium*, *Coryphodon*, and *Phenacodus*, probably resulted from counting individual specimens rather than the minimum number of individuals necessary to account for the specimens.

Several species listed here have not previously been recovered from Lost Cabin deposits in the Wind River Basin. *Talpavus sullivanii*, *Lophiparamys woodi*, *Antiacodon vanvaleni*, and *Bunophorus gazini* are new species, described here. Other species, including *Peratherium* cf. *P. chesteri*, *Peratherium comstocki*, *Phenacolemur jepseni*, *Viverravus lutosus*, *Uintacyon asodes*, *Oödetes* sp., and *Homogalax protapirinus*, although new to the Wind River Lost Cabin, are known from other faunas of Lostcabinian age, or from both older and younger deposits. The inclusion of *Entomolestes nitens*, *Palaeosinopa lutreola*, *Palaeosinopa* cf. *P. veterrima*, *Phenacolemur citatus*, *Microsyops latidens*, *Lophiparamys woodi*, and *Miacis jepseni* extends the range of these species (or the lineages to which they belong) upward into the Lostcabinian from older deposits. The recovery of *Myolestes dasypelix*, *Antiacodon vanvaleni*, and *Apatemys* cf. *A. bellus* extends the ranges of these species or lineages downward into the Lostcabinian from younger horizons.

The lower vertebrates of the Lost Cabin have not been studied, but the fauna is known to contain *Lepisosteus*, *Trionyx*, *Baptemys*, *Glyptosaurus*, *Saniwa*, *Boavus*, *Jepsibaena*, and a crocodile.

### FAUNAL CORRELATION

#### LYSITE

Comparison of the Lost Cabin fauna with the Wind River Lysite fauna is relatively easy. Both are represented by large collections, and the Lysite fauna has been recently studied (Guthrie, 1967a). They are so similar in age, location, and depositional condition that paleoecological differences can be discounted. Most of the differences between

these two faunas may be due only to sampling error. Although the Lysite genera *Franimys*, *Thryptacodon*, *Apheliscus*, *Anacodon*, and *Wasatchia* have not been found in Lost Cabin deposits, these genera are rare in the Lysite and may eventually be recovered in the Lost Cabin. Similarly, among the lineages first appearing in the Lost Cabin, *Oödetes*, *Microsyops lundeliusi*, *Myolestes*, *Loveina*, *Selenaletes*, and *Hyrachyus* are rare and may also occur in the Lysite fauna. Only *Lambdotherium*, *Eotitanops*, and *Shoshonius* are so common at first appearance in the Lost Cabin that their presence can be attributed to immigration. Three other species, *Diacodexis secans*, *Microsyops scottianus*, and *Phenacolemur jepseni* make their first appearance in the Lost Cabin deposits and coexist with the species from which they are descended. This suggests immigration into the Wind River Basin after very recent allopatric speciation.

All other Lost Cabin species are members of lineages that first appear in earlier strata. Several of these lineages undergo nomenclatural changes, arbitrarily placed in the interval between the Lysite and Lost Cabin. On the generic level, these include *Pelycodus-Notharctus*, *Oxyaena-Patriofelis*, *Probathyopsis-Bathyopsis*, and *Ectoganus-Stylindodon*. Nomenclatural changes at the specific level occur in the genera *Absarokius*, *Palaeictops*, *Prolimnocyon*, *Paeneprolimnocyon*, *Didymictis*, *Uintacyon*, *Hyopsodus*, *Coryphodon*, and *Esthonyx*.

Between the Lysite and Lost Cabin horizons, tooth size in most species remains constant or increases, the former situation occurring more often in smaller forms, the latter in larger species. There are only seven instances of decrease in size with time. Five of these (*Diacodexis metsiacus*, *Hyracotherium vasacciense*, *Phenacolemur jepseni*, *Phenacodus vortmani*, and *Microsyops latidens*) may be due to newly arisen intra-generic competition with a larger species. In *Hyracotherium craspedotum*, decrease in size is probably due to competition from the new immigrant, *Lambdotherium*. The reason for the other instance of size decrease, in *Phenacodus primaevus*, is not clear.

#### NEW FORK, LOWER HUERFANO

The New Fork faunas of West (1968) and Gazin (1962) and the lower Huerfano (A level) of Robinson (1966) are the same age as the fauna from the type Lost Cabin area in the Wind River Basin. Almost all differences among these faunas are either attributable to the rarity of the species concerned or are differences only in taxonomic viewpoint among the authors. The only real differences seem to be the presence

of *Hexacodus* in southern Wyoming and nowhere else, the absence of *Notharctus venticolus* in West's samples, and the absence of *Shoshonius* from Gazin's New Fork sample. The last two differences may be due to small sample size.

#### LA BARGE

The La Barge fauna (Gazin 1952, 1962) is generally considered older than the New Fork faunas. It is also older than the Wind River Lost Cabin fauna. Although comparison of measured samples among these faunas is not possible at present, in several lineages the form found in the Wind River Lysite, rather than the Lost Cabin form, is present in the La Barge. These include *Prolimnocyon elisabethae*, *Oxyaena*, *Palaeictops pineyensis*, and *Thryptacodon*, a genus not known in the Lost Cabin or its equivalents. The only other differences among these faunas that cannot be ascribed to sampling omissions of rare forms are the presence of *Knightomys senior* and *Hexacodus* and the absence of *Shoshonius* and *Phenacodus primaevus* in the La Barge, whereas *Knightomys depressus*, *Antiacodon*, *Shoshonius*, and *Phenacodus primaevus* are present in the Wind River Lost Cabin and *Hexacodus* is absent. The distributional differences of *Hexacodus* and *Knightomys* are probably due to paleoecological or geographic factors, while those of *Phenacodus* and *Shoshonius* may be due to the earlier age of the La Barge deposits.

#### UPPER HUERFANO, CATHEDRAL BLUFFS

These faunas have been shown to contain species of Bridgerian affinities (Gazin, 1962; Robinson, 1966; West, 1969b), and are clearly younger than the Wind River Lost Cabin fauna. Among common species, the most important differences are the appearance of *Palaeosyops*, *Scenopagus*, and *Trogosus* in these faunas, evolutionary advance in several lineages including changes on the specific level in *Viverravus*, *Miacis*, and *Hyopsodus*, and the absence in these faunas of such typical Lostcabinian forms as *Lambdotherium*, *Heptodon*, *Esthonyx*, and probably *Phenacolemur* and *Palaeictops*.

#### SYSTEMATIC REVIEW

##### Order Marsupialia

##### Family Didelphidae

##### *Peratherium* cf. *P. chesteri* Gazin, 1952

Two isolated teeth (CM 22000, 22001, fig. 2a, b) are the first Wind



River record of this La Barge species. There are at least two lineages of didelphids throughout the early Eocene. A lineage of small individuals includes *Peradectes protinnominatus* (McKenna, 1960a), from the Four Mile fauna, and *Peratherium innominatum* (Simpson, 1928) from the Bridger formation. *Peratherium chesteri* fits into this lineage.

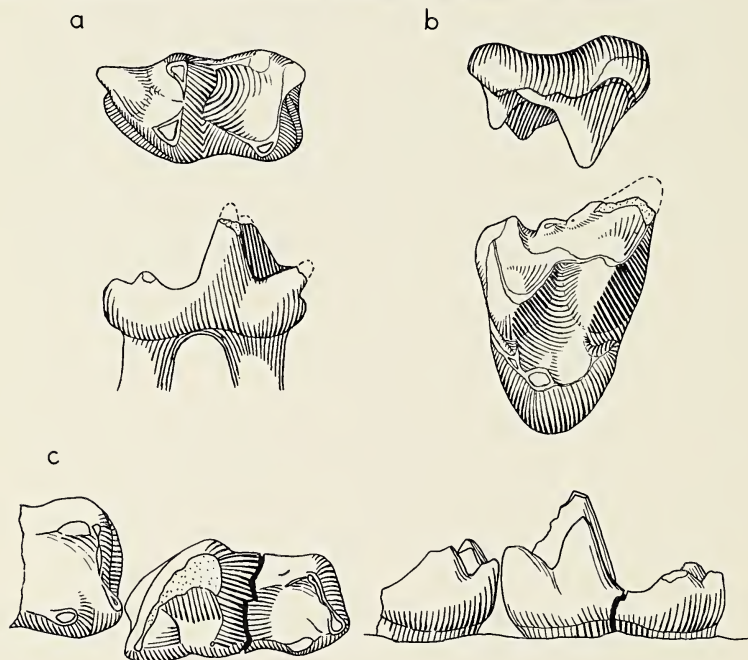


Fig. 2a-b. *Peratherium* cf. *P. chesteri*. a. CM 22001, LM<sub>2</sub> or LM<sub>3</sub>. b. CM 22000, LM<sub>1</sub> or LM<sub>2</sub>. c. *Peratherium comstocki*, CM 21126, LM<sub>2</sub>-M<sub>3</sub>. All  $\times 10$ .

### *Peratherium comstocki* Cope, 1884

A jaw fragment containing M<sub>3</sub> and part of M<sub>2</sub>, CM 21126 (fig. 2c), is referable to *P. comstocki*. M<sub>3</sub> measures 3.05 mm. in length and 1.55 mm. in trigonid width. Two Wasatchian species of *Peratherium*, *P. comstocki* and *P. edwardi*, are near this size. This specimen is nearer to the former in size.

Order Insectivora

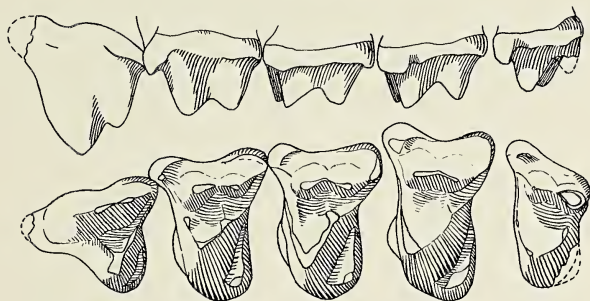
Family Leptictidae

### *Palaeictops bicuspis* (Cope, 1880)

The Lost Cabin individuals of *Palaeictops* (table 2) are clearly

larger than the Wind River Lysite specimens of *Palaeictops*, referred to *P. pineyensis* by Guthrie (1967a). One specimen (PU 13436) is figured here to augment Matthew's figures (1918, figs. 3-5) of the type specimen, and to show the variation that occurs in the Lost Cabin sample.

a



b

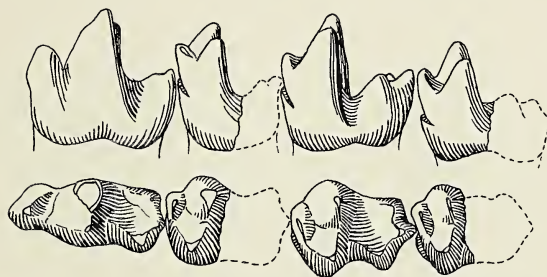


Fig. 3. *Palaeictops bicuspis*, PU 13436. a. LP<sup>3</sup>-M<sup>2</sup>, RM<sup>3</sup> reversed. b. LP<sub>4</sub>-M<sub>3</sub>. x5.

### *Palaeictops multicuspis* (Granger, 1910)

I have followed Van Valen (1967) in placing this species in *Palaeictops*, and I consider *P. multicuspis* ancestral to *P. bridgeri*. Only the type specimen, AMNH 14741, and two isolated molars, CM 22007 and CM 22008, the latter from the Lysite Member of the Wind River formation, are known. Complete measurements of the type specimen are presented here (table 2).

### Family Apatemyidae

#### *Apatemys whitakeri* (Simpson, 1954)

Several specimens from the Lost Cabin confirm the presence of this species, previously known only from an edentulous jaw referred to

*Teilhardella* sp. by White (1952). Measurements of this sample are presented in table 3. One specimen exhibits a greater degree of reduction of the paraconid on the lower molars than was previously known in this species (fig. 4a).

*Apatemys* cf. *A. bellus* Marsh, 1872

An edentulous jaw of an apatemyid (CM 22013) resembles this species in size more closely than it does *A. whitakeri*. This specimen also appears to have had a two-rooted  $P_4$ , a condition present in *A. bellus* but absent in *A. whitakeri*.

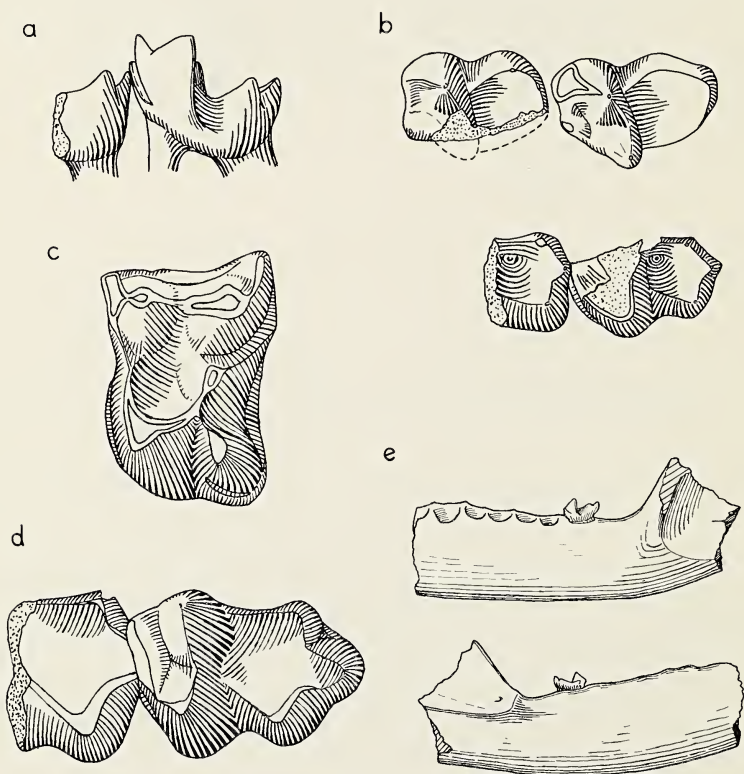


Fig. 4. a. *Apatemys whitakeri*, CM 22010,  $RM_2-M_3$ , x10. b-c. *Entomolestes nitens*. b. CM 22014,  $LM_2-M_3$ , x15. c. CM 22015,  $LM^2$ , x15. d-e. *Myolestes dasypelix*. d. CM 22018,  $LM_2-M_3$ , x15. e. CM 22016, left jaw with  $M_3$ , x5.



## Family Adapisoricidae

*Entomolestes nitens* Matthew, 1909

The two specimens illustrated (CM 22014, 22015, fig. 4b, c) represent the first Lost Cabin record of this genus. These teeth do not differ significantly from specimens referred to this species by Matthew (1918), McKenna (1960a), and Guthrie (1967a). I do not agree with Robinson (1968) that this species should be included in *Scenopagus*. The upper molars of *E. nitens* and *Scenopagus* are quite different, especially in the development of the hypocone.

*Myolestes dasypelix* Matthew, 1909

Three jaws (CM 22016-22018) represent the first Lost Cabin record of this genus. These specimens agree with the Bridger type specimen of this species, and with material referred to this species by McKenna (1960b) in both size (table 4) and dental characteristics, and in the configuration of the posterior part of the mandible (fig. 4d, e).

*Talpavus sullivan*<sup>1</sup>, new species

TYPE: AC 2666, right ramus with M<sub>2,3</sub>.

HYPODGM: Type specimen and CM 22019, 22020, 22023, isolated upper molars; CM 22021, left M<sub>3</sub>; and CM 22022, left M<sub>1</sub>.

HORIZON AND LOCALITY: Type, Lysite deposits in the Wind River Basin; referred specimens, Lost Cabin deposits in the Wind River Basin.

DIAGNOSIS: Compared to *T. nitidus*, paraconids on lower molars more medial, anterior cingula smaller, cusps not as high; on the upper molars, hypocones not as well developed; anterior cingula smaller and upper molars narrower in width.

DISCUSSION: The type specimen was figured by Guthrie (1967a) as *Talpavus* sp. (misspelled *Tulpavus*). Measurements and figures of the other specimens are presented in table 5 and fig. 5a-d. This species is ancestral to *T. nitidus*. The specimen referred to *Talpavus* sp. cf. *T. nitidus* by Robinson (1966) may belong to *T. sullivan*. The specimen referred to ? "*Nyctitherium*" sp. by McKenna (1960a), while smaller than *T. sullivan* and exhibiting a less developed hypocone, might be a likely ancestral form for *T. sullivan*. It probably should be referred to *Talpavus*, although Van Valen (1967) thought it represented a distinct genus.

<sup>1</sup>Etymology. Named for Frank R. Sullivan of Arminto, Wyoming, whose courteous assistance made much of our field work possible.

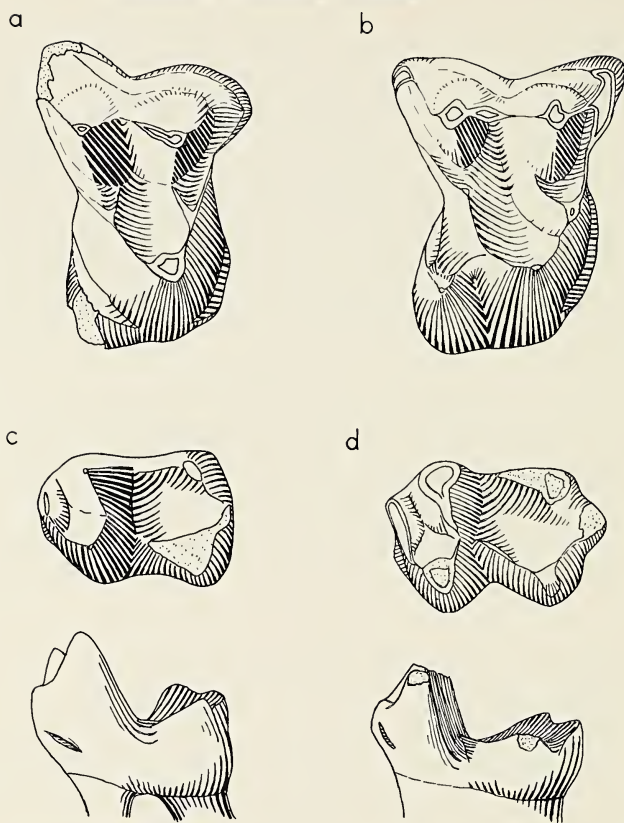


Fig. 5. *Talpavus sullivani*, new species. a. CM 22020, ?RM<sup>2</sup>. b. CM 22019, ?RM<sup>1</sup>. c. CM 22022, LM<sub>1</sub>. d. CM 22021, LM<sub>3</sub>. All x15.

### Family Pantolestidae

#### *Palaeosinopa didelphoides* (Cope, 1881)

The Lost Cabin specimens referable to this genus, like the sample from the Gray Bull deposits in the Big Horn Basin, belong to three species. *Palaeosinopa didelphoides*, the medium-sized species, is the common form in both deposits. The Gray Bull specimens differ from the Lost Cabin specimens in possessing larger paraconids on the lower molars, greater expansion of the metastylar shelf on the upper molars (Van Valen, 1967, fig. 6a-c) and in being slightly smaller (table 6). Gazin (1962) pointed out the similarities between this species and *Pantolestes longicaudus*, which the Lost Cabin sample approaches in morphology.

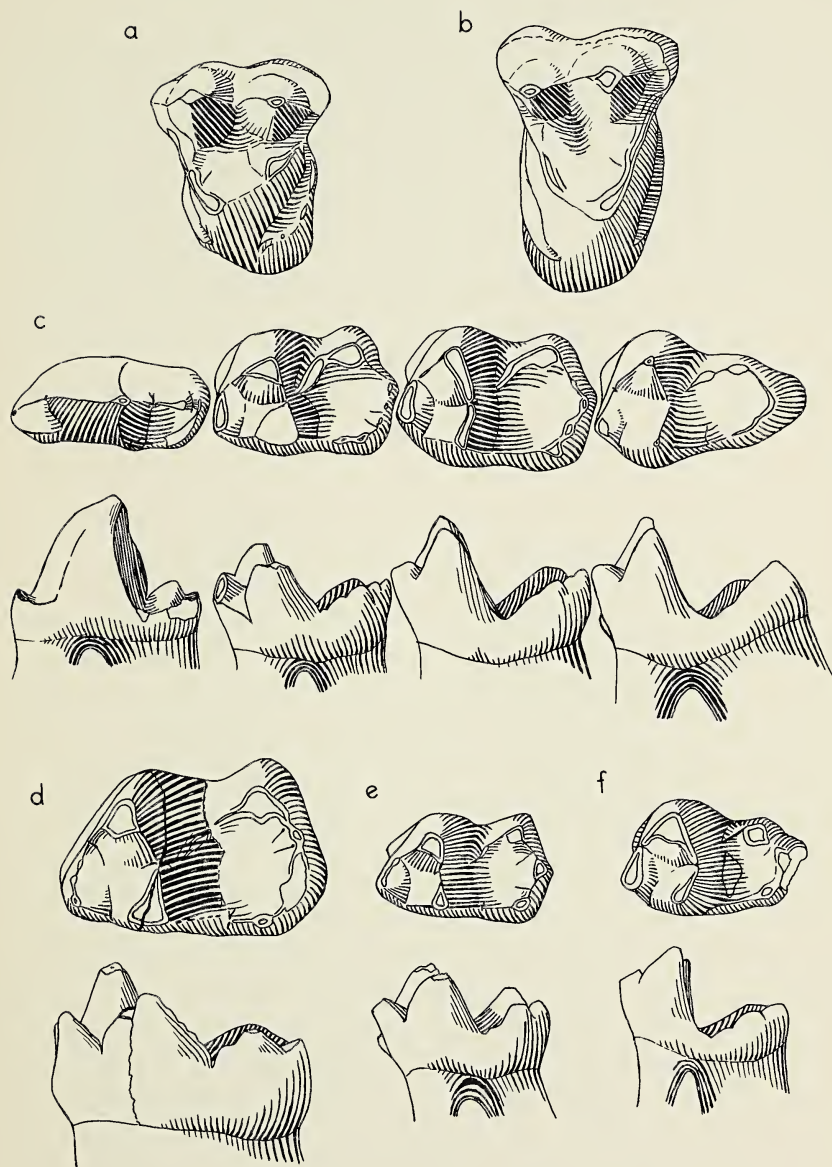


Fig. 6. a-c. *Palaeosinopa didelphoides*. a. CM 22031, LM<sup>1</sup>. b. CM 22031, RM<sup>2</sup>. c. Composite of CM 22036, LP<sub>4</sub>-M<sub>1</sub> reversed; CM 22027, RM<sub>2</sub>; and CM 22030, RM<sub>3</sub>. d. *Palaeosinopa* cf. *P. veterrima*, CM 22042, RM<sub>1</sub>. e-f. *Palaeosinopa lutreola*. e. CM 22041, RM<sub>1</sub>. f. CM 22040, RM<sub>3</sub>. All x5.



*Palaeosinopa lutreola* Matthew, 1918

A few isolated teeth (CM 22039-22042, fig. 6e, f), too small to be included in *P. didelphoides*, are referred to this smaller Gray Bull species. The paraconids on the lower molars are larger than in *P. didelphoides*.

*Palaeosinopa* cf. *P. veterrima* Matthew, 1901

An isolated RM<sub>1</sub>, CM 22042 (fig. 6d), seems referable to this species. Although clearly larger than described members of the genus, this tooth which measures 7.20 mm. in length and 4.18 mm. in width, is intermediate between *P. veterrima* of the Gray Bull and *Pantolestes phocipes* of the Bridger deposits. It agrees with these species in having the paraconid directed upward, not forward as in other species of *Palaeosinopa* and *Pantolestes*.

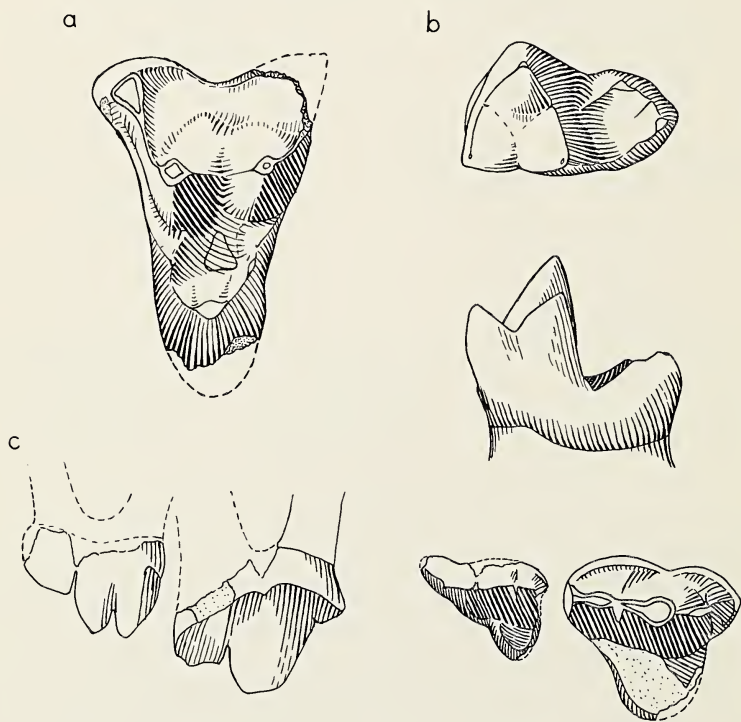


Fig. 7. a-b. *Didelphodus altidens*. a. CM 22048, LM<sup>2</sup>, x10. b. CM 22043, RM<sub>3</sub>, x10. c. *Patriofelis tigrinus* CM 22050, RM<sup>1</sup>; AMNH 14779, RP<sup>4</sup>, x1.

## Order Deltatheridia

## Family Palaeoryctidae

*Didelphodus altidens* (Marsh, 1872)

Although both species of *Didelphodus* were recorded from the Lost Cabin by Van Valen (1966), the only specimen referred to *D. absarokae* (USNM 18433) is a specimen of *Paeneprolimnocyon*. Lower molars of these two genera are nearly identical. In *Paeneprolimnocyon* the distance from the crown of the talonid to the base of the enamel on the side of the tooth is shorter than in *Didelphodus*, and the paraconid points anteriorly rather than upward as it does in *Didelphodus*.

Several of the isolated Lost Cabin teeth referred to *D. altidens* approach the Bridgerian species, *D. absarokae*, in morphology (fig. 7a, b).

## Family Oxyaenidae

*Patriofelis tigrinus* (Cope, 1880)

In addition to the type specimen (AMNH 4805), four additional specimens from the Lost Cabin are known: AMNH 14778 and 14779, and CM 22050 and 22051. Denison (1938) resurrected the name *Protopsalis* for this species but it is so close to *Patriofelis* in size and in the shape of the upper molars (fig. 7c) and lower molars that generic separation seems unnecessary. I agree with Denison that *P. tigrinus* is probably not ancestral to any other species of *Patriofelis*. *Patriofelis tigrinus* is certainly closer to *Patriofelis* than to its ancestral genus *Oxyaena*, and the differences between these two genera are not great enough to merit separate generic assignment for this intermediate form.

*Oxyaena* has been recorded from deposits of Lostcabinian age in the Wind River, Huerfano and Green River Basins. A specimen from the North Fork of the Wind River (MCZ 3433), described as the type of *Oxyaena ultima* by Denison (1938) and considered a synonym of *O. forcipata* by Guthrie (1967a) is from a Lysite horizon, and not from a Lost Cabin horizon as Denison stated (and as the specimen is labeled). No material of either *Lambdaotherium* or *Eotitanops*, or any other species that would indicate a Lostcabinian age was found with this specimen of *Oxyaena*, and the fauna that was collected with it suggests a Lysite age. All other oxyaenids from the Wind River Lost Cabin are referable to *Patriofelis*.

## Family Hyaenodontidae

*Prolimmnocyon antiquus* Matthew, 1915

The Lost Cabin sample of this species, previously known only from a nearly edentulous type specimen, is now fairly large. Measurements and illustrations of these specimens are presented in table 7 and fig. 8a. The sample corresponds well with the specimen referred to this species from the New Fork horizon by Gazin (1962). This species is clearly larger than the ancestral Lysite and La Barge species, *P. elizabethae*.

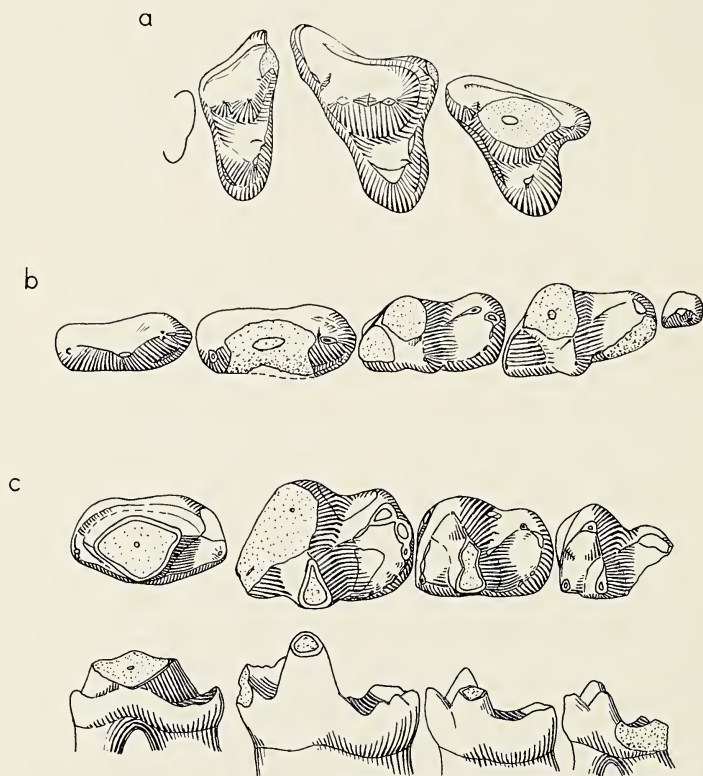


Fig. 8. a-b. *Prolimmnocyon antiquus*. a. CM 22052, RP<sup>4</sup>-M<sup>2</sup>, x3. b. Composite of PU 19357, LM<sub>1</sub>-M<sub>2</sub> reversed; CM 22054, RP<sub>3</sub>-P<sub>4</sub>, M<sub>3</sub>; x3. c. *Paeneprolimmnocyon amissadomus*, composite of CM 22058, RP<sub>4</sub>-M<sub>1</sub>; CM 21202, RM<sub>2</sub>; and CM 22059, LM<sub>3</sub> reversed. x5.

*Paeneprolimmnocyon amissadomus* Guthrie, 1967

Several additional specimens of *Paeneprolimmnocyon* have been dis-



covered since my description of the type specimen (table 8, fig. 8c). These include specimens previously referred to *Didelphodus*. Van Valen's (1969) referral of *Paeneprolimnocyon* to the Hyaenodontinae is sound but I disagree with his view that *P. amissadomus* is synonymous with *P. iudei*.

*Prototomus multicuspis* Cope, 1875

The remains of four individuals of a small species of proviverrine creodont have been recovered from the Lost Cabin. These specimens, which include the type specimen of *P. vulpecula*, are referred to *P. multicuspis*. I consider these two species synonymous and the latter name has priority.

*Tritemnodon strenua* (Cope, 1875)

Large proviverrine creodonts from the Lost Cabin have previously been referred to *Tritemnodon whitiae*, *T. strenua*, and *T. hians*. Pending a revision of this group, I consider the former two species synonymous. The variation in this combined sample is about the same as in most species. The one Lost Cabin specimen referred to *T. hians* by Matthew (1915a, AMNH 12786) is placed in *T. strenua*, although it is larger than the other specimens and may represent another species.

Order Primates

Family Notharctidae

*Notharctus nunienus* (Cope, 1881)

*Notharctus venticolus* Osborn, 1902

These species are well known, therefore only measurements of the Lost Cabin sample are presented here (tables 9, 10). The small samples from both the Green River (West, 1968) and Huerfano (Robinson, 1966) sediments of Lost Cabin age contain larger specimens of *N. nunienus* than are found in the Wind River Basin. I have previously treated the La Barge species *N. limosus* as a synonym of *N. nunienus* (Guthrie, 1967a).

Family Omomyidae

*Shoshonius cooperi* Granger, 1910

Molars of this species are well known and only the lower premolars, previously undescribed, are figured here (fig. 9a). As expected, P<sub>3-4</sub> are simpler in construction but basically similar to those in the descendent Bridgerian genus *Washakius*. The paraconid and metaconid are distinct

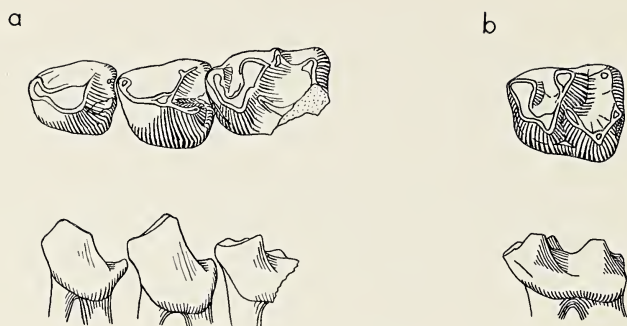


Fig. 9. a. *Shoshonius cooperi*, CM 22105, LP<sub>3</sub>-M<sub>1</sub>, x7.5. b. *Loveina zephyri*, CM 22130, LM<sub>2</sub>, x7.5.

on P<sub>4</sub>, and there is a ridge posterior from the metaconid, but there is no metastylid as on the molars. Two ridges run between the protoconid and the posterior cingulum, a buccal one connected to the protoconid and a lingual one connected to the posterior cingulum. A deep groove separates these ridges from each other. The metaconid is absent on P<sub>3</sub> and this tooth is generally simpler than P<sub>4</sub>. Roots anterior to P<sub>3</sub> indicate that P<sub>2</sub> was single-rooted, and that there were three teeth anterior to P<sub>2</sub>, probably a large canine and two small incisors, as in *Washakius*. There is a single mental foramen below P<sub>3</sub>.

*Loveina zephyri* Simpson, 1940

In addition to the type specimen (AMNH 32517) and the maxilla (MCZ 3495) described as *Tetonius barbeyi* (Seton, 1940; Gazin 1958) I refer CM 22130, an isolated M<sub>2</sub> (fig. 9b), to this species. This latter specimen is the first from the Alkali Creek area. The other specimens are from the northwestern portion of the Wind River Basin. This species is similar to a host of other Eocene omomyids, especially *Omomyis sheai*, with which *Loveina* may be congeneric. The present material is too fragmentary to allow this determination.

Family Anaptomorphidae

*Absarokius noctivagus* Matthew, 1915

This species has been well described and figured (Matthew, 1915c; Gazin, 1958, 1962). Measurements of the Lost Cabin sample are presented in table 12.

## Family Paromomyidae

*Phenacolemur citatus* Matthew, 1915

Two jaws, CM 22134 and 22136, and two isolated teeth, CM 22133, 22135 (table 13, fig. 10a, b), are referable to this species. These teeth are the size of *P. praecox* of the lower Gray Bull but are advanced in the reduction of the talonid on  $P_4$  and in the reduction of the paraconid on  $M_1$ . They are similar to teeth from the Lysite population of *P. citatus* and are referred to this species despite their large size. The Lost Cabin sample of *P. citatus* thus indicates a reversal of the trend toward smaller size that this lineage shows from the Gray Bull to the Lysite (Guthrie, 1967a). This reversal may be due to competition from the smaller, contemporaneous species, *P. jepseni*.

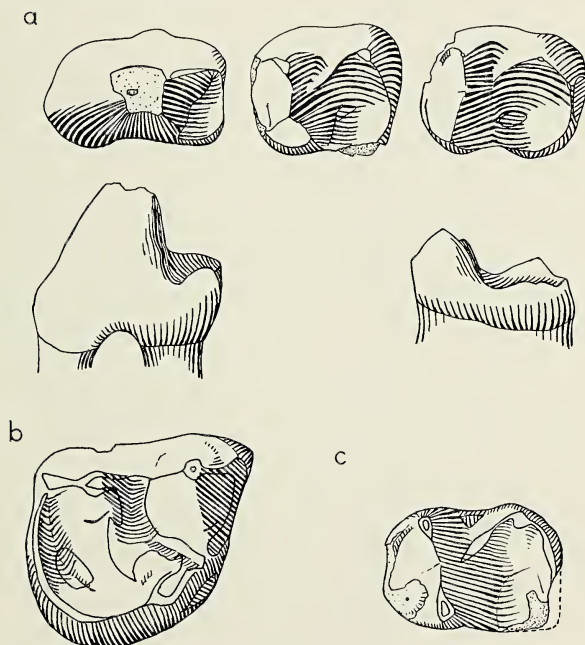


Fig. 10. a-b. *Phenacolemur citatus*. a. CM 22136,  $RP_4-M_1$ ; CM 22134,  $RM_2$ . x7.5. b. CM 22135,  $?LM_1$ , x7.5. c. *Phenacolemur jepseni*, CM 22132,  $RM_1$ , x10.

*Phenacolemur jepseni* Simpson, 1955

A single isolated  $RM_1$  (CM 22132, table 13, fig. 10c) is too small to be included in the Lost Cabin sample of *P. citatus* and is referred to this



smaller New Mexican species with which it agrees in configuration. The Wind River Lost Cabin specimen is closer to the Huerfano subspecies, *P. j. simpsoni* (Robinson, 1966), in size than to the New Mexican type specimen.

Family Microsyopidae

*Microsyops latidens* (Cope, 1882)

*Microsyops scottianus* (Cope, 1881)

*Microsyops lundeliusi* (White, 1952)

These species have recently been reviewed by Szalay (1969a). Although a larger sample of *M. scottianus* is now known from the Lost

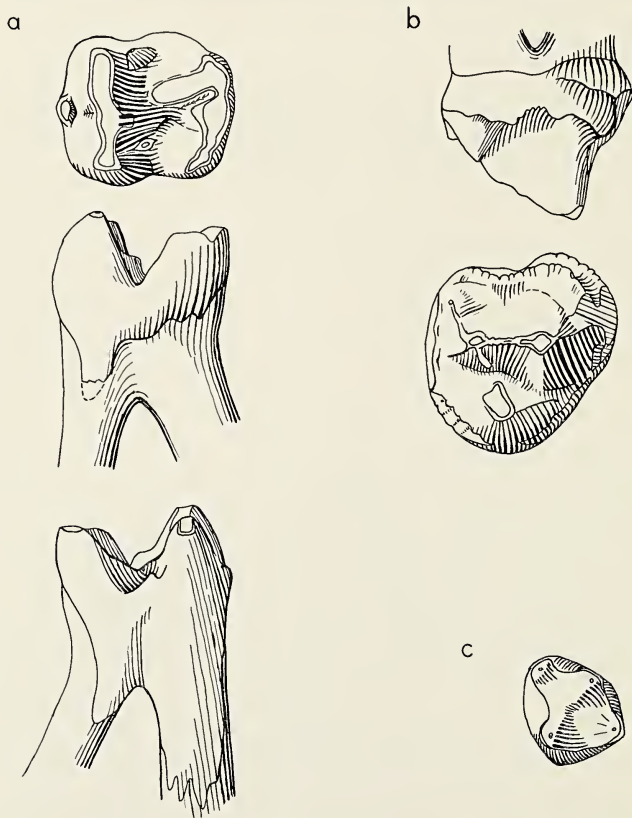


Fig. 11. a-b. *Stylinodon cylindrifera*. a. CM 22303, ?RDP<sub>4</sub>. b. CM 22304, ?RDP<sub>4</sub>. x2.5. c. *Tubulodon taylori*, CM22032, RM<sub>3</sub>, x7.5.

Cabin, Szalay's data for the lower teeth are accurate. Measurements of upper teeth of *M. scottianus*, previously poorly represented in collections, are presented in table 14. Two isolated teeth (CM 22258), too small to be *M. scottianus*, are assigned to *M. latidens*. They agree with the Lysite sample of *M. latidens* in size and configuration. Szalay (1969a) recorded *M. latidens* in the La Barge fauna, but this species has not been previously recorded in the Wind River Lost Cabin fauna. If these teeth actually are *M. latidens*, it would appear that *M. scottianus* did not evolve from *M. latidens* in the Wind River Basin, but rather migrated into the basin, replacing *M. latidens*. I follow Szalay in considering *Cynodontomys* a synonym of *Microsypops*.

#### Order Taeniodonta

##### Family Stylinodontidae

##### *Stylinodon cylindrifer* (Cope, 1881)

The type specimen (AMNH 4180) and several other specimens, all tooth fragments (AMNH 14743-14745, USNM 18440), are known from the Wind River Lost Cabin. These specimens are too fragmentary to allow me to determine whether this species is distinct from *Ectoganus simplex* of the Lysite and earlier horizons. Two unworn, isolated teeth (CM 22303, 22304, fig. 11a, b), probably deciduous premolars, are also referred to *S. cylindrifer*. They agree in shape with figures of milk teeth of *Ectoganus gliriformis* (Gazin, 1936).

#### Order Edentata

##### Family Metacheiromyidae

##### *Palaeonodon ignavus* Matthew, 1918

In addition to the three lots of foot bones mentioned by Matthew (1918) a right astragalus (CM 22307) is now known. Despite the size variation among these specimens, all are referable to *P. ignavus*.

#### Order Edentata, *incertae sedis*

##### *Tubulodon taylori* Jepsen, 1932

A second specimen of *Tubulodon* (CM 22302), consisting of a jaw fragment with  $M_3$ , was recovered from locality 1 (the type locality). This tooth, the first known  $M_3$ , is illustrated in fig. 11c. The tooth is single-rooted and measures 1.7 mm. in length and 2.0 mm. in width. Although all enamel is absent from the crown, a pattern of four cusps is visible in the dentine. Jepsen (1932) noted this condition of unworn

dentine cusps in the type specimen and suggested that the enamel never covered the tooth crown. On the Carnegie Museum specimen wear on some enamel edges can be seen, especially near the posterior margin and near the cusps, but as the enamel layer nears the tooth valleys, it thins out without evidence of wear. Cusp homologies, as in the type specimen, are not clear, but the same cusps noted by Jepsen on the anterior molars, except for the paraconid, are present on  $M_3$ .

### Order Rodentia

The taxonomic treatment of early Eocene rodents in this paper differs from that of Wood (1962, 1965) in several respects. Several samples that I view as single biological species include variants suggestive of later taxa. Wood treats these variants as separate subspecies, species, or genera leading to or included in later taxa. For instance, Wood (1962: 38, 55), separated contemporaneous samples of *Paramys copei* and *Paramys excavatus* into subspecies on morphological grounds, to indicate that within these species there are trends toward several descendent species. I agree with Gazin (1956:15), "in opposing a concept which recognizes more than one subspecies of the same form coexisting in time at the same geographical locality." Furthermore, Wood recognizes as distinct species or genera forms that I consider variants of one species. He separated some specimens from *Paramys excavatus* and described them as *Reithroparamys atwateri*, because these specimens tend toward the genus *Reithroparamys*. He stated (1962:55), however, that *P. excavatus obliquidens* is no more than subspecifically distinct from *Reithroparamys atwateri*. I treat specimens referred to *R. atwateri* as variants of the population of *Paramys excavatus*.

The effect of this change in taxonomy is to eliminate from the early Eocene many species that Wood considered first representatives of later Bridgerian genera. I regard the specimens upon which these species were based as variants of early Eocene species.

One other difference between my treatment and that of Wood (1962, 1965) is in the identification of isolated incisors. I have presented measurements of only those incisors that are associated with cheek teeth, or that belong to a species in which distinct shape and size allow identification. Many isolated incisors, especially those of *Paramys*, cannot be identified as to species because there is considerable variation in incisor size (fig. 12).



## Family Paramyidae

*Paramys copei* Loomis, 1907

Wood (1962) divided *Paramys copei* into three subspecies, two of which, *P. copei copei* and *P. c. major*, are found in the Lost Cabin de-

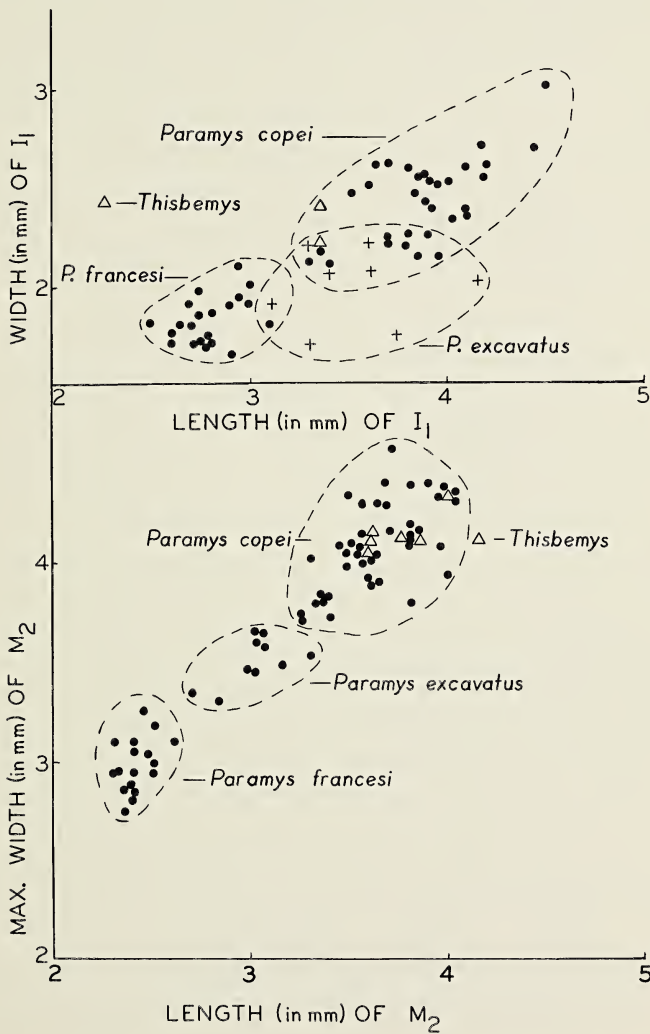


Fig. 12. Measurements of M<sub>2</sub> and I<sub>1</sub> of Lost Cabin members of the genus *Paramys*. Only incisor teeth associated with molar teeth are included.

posits. These subspecies are not recognized (see comment above). Since Wood presented measurements of *P. copei* separated by subspecies and not by horizon, measurements for the entire Lost Cabin sample are presented in table 15.

Wood (1962) described *Paramys wortmani* from several specimens that exhibit variation toward the Bridgerian species *P. delicatior* and *P. delicatus*. These features, an entoconid separate from the posterior cingulum on the lower molars, wider incisors, reduced trigonid basins, and a ridge from the entoconid into the talonid basin, are not much advanced from the condition found in *P. copei*. *Paramys wortmani* and *P. copei* are identical in size, and the separation on morphological ground appears, after study of the larger Lost Cabin sample now available, to be illusory. Wood noted that *P. wortmani* could be considered a subspecies of *P. copei* or of *P. delicatior*. The specimens referred to *P. wortmani* are better considered extreme variants within *P. copei* toward the Bridgerian species mentioned above.

In the original description of *Thisbemys perditus*, Wood noted that more than one species may be represented. The Lost Cabin sample (table 18, fig. 12) consists mostly of specimens identical in size with *Paramys copei*. Indeed the difference in the amount of crenulation on the cheek teeth is the only characteristic that separates these two species. A few small specimens referred to *Thisbemys perditus* are more the size of *Paramys excavatus*, and again, these specimens are only separable from *P. excavatus* in that their teeth are more crenulated. This crenulation may represent only individual variation within *Paramys copei* and *P. excavatus*, rather than a generic difference. Certainly the specimens referred to *Thisbemys perditus* do not approach the Bridgerian members of *Thisbemys* in the degree of corrugation, but look more like extreme variants of early Eocene *Paramys*. I regard specimens referred to *Thisbemys perditus*, especially those from the Wind River Basin, as crenulated variants within *Paramys copei* and *Paramys excavatus*. Enough doubt exists, however, and I have accordingly not included specimens possibly referable to *Thisbemys* in the *Paramys* measured samples.

#### *Paramys excavatus* Loomis, 1907

Wood (1962) referred Gray Bull and Lysite specimens to the genus *Reithroparamys* (*R. atwateri*) although they were considered by him only subspecifically distinct from a Gray Bull subspecies of *Paramys excavatus*. Whether the Gray Bull and Lysite samples of *Paramys exca-*

*vatus* contain within them morphological variants toward, or more accurately, foreshadowing, *Reithroparamys*, or are composed of sibling species inseparable except on minor characters is immaterial. The samples should be considered a single species rather than split into two species on arbitrary grounds. The view that these samples represent a single species, with variants foreshadowing *Reithroparamys*, is favored by two observations. First, the total amount of variation in the samples

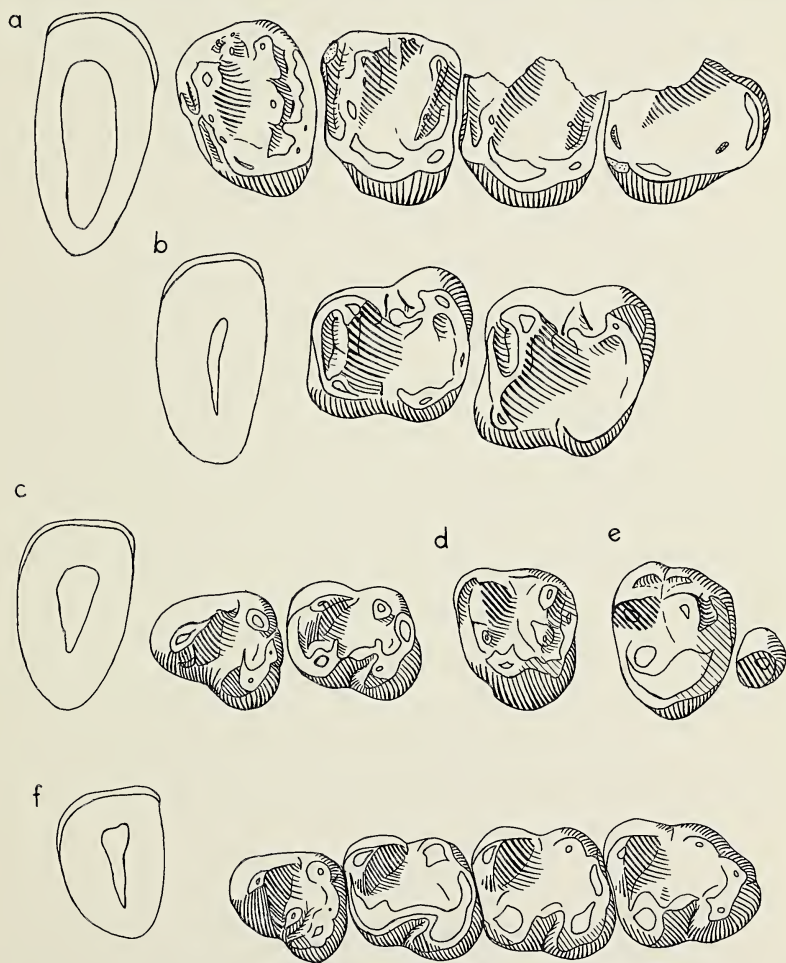


Fig. 13. a-b. *Paramys excavatus*, CM 22211. a. LI<sup>1</sup>, P<sup>4</sup>-M<sup>3</sup>. b. RI<sub>1</sub>, M<sub>1</sub>-M<sub>2</sub>. c-f. *Paramys francesi*. c. CM 22227, LI<sub>1</sub>, P<sub>4</sub>-M<sub>1</sub>. d. CM 22229, LM<sup>1</sup>. e. CM 22231, RP<sup>3</sup>-P<sup>4</sup>. f. CM 22222, LI<sub>1</sub>, P<sub>4</sub>-M<sub>3</sub>. All  $\times 7.5$ .



does not increase from the Gray Bull to the Lost Cabin as might be expected if the samples were composed of sibling species. Second, variations toward the genus *Reithroparamys* (in such features as separation of the entoconid, narrowing of the trigonid basin, and development of a ridge extending into the talonid basin from the entoconid) are also found in the closely related species *Paramys copei* and *Paramys francesi*. I therefore feel confident in considering *Reithroparamys atwateri* a synonym of *Paramys excavatus*.

Two species of *Reithroparamys* have been reported from deposits of Lostcabinian age. One of these, *R. debequensis*, exhibits an entoconid well separated from the posterior cingulum, and a prominent ridge from the entoconid into the central basin of the lower molars—in short, the characteristic features of the Bridgerian members of this genus. There seems to be little doubt that this species is correctly referred to *Reithroparamys*, although the single Lysite specimen referred here (USNM 22380) may represent *Paramys*.

*Reithroparamys pattersoni*, the other Lost Cabin species, is not so clearly referable to *Reithroparamys*. The lower teeth of this species do not exhibit the fully developed features of the genus, but rather show variations from a *Paramys* pattern toward the *Reithroparamys* condition. Wood (1962) considered *R. pattersoni* a possible descendant of *R. atwateri* and not ancestral to any other species of *Reithroparamys*. I think *R. pattersoni* consists of variants toward *Reithroparamys* selected from the Lost Cabin sample of *Paramys excavatus*. On the basis of the larger amount of material currently available from the Lost Cabin, the division between *R. pattersoni* and *Paramys excavatus* seems not a natural one.

*Paramys excavatus*, like *Paramys copei*, is a “stem” rodent species containing within it variants suggestive of several Bridgerian rodent species. Measurements of the Lost Cabin sample of *Paramys excavatus* are given in table 16. Associated upper and lower teeth of *P. excavatus*, the first such association known, are illustrated in fig. 13a, b.

#### *Paramys francesi* Wood, 1962

This species is well represented in the Lost Cabin (table 17). The recently recovered specimens (figs. 12, 13c-f) differ from the type specimen in two respects: the entoconid is less separated from the posterior cingulum than in the type, and the protoconid on P<sub>4</sub> is very poorly developed. *Paramys francesi* was considered by Wood to be closely re-

lated to *Sciuravus*, a position with which I disagree. *Paramys francesi* is almost certainly ancestral to *Paramys wyomingensis* (West, 1969a; Wood, 1962 as *Microparamys*), *P. wyomingensis* not arising from *P. copei* as suggested by West. It is possible that *P. francesi* is descended from Wood's (1962) *Microparamys* sp. A., a species that should also be referred to *Paramys*.

The upper teeth referred by Wood (1962) to *P. francesi* (AEW 9363, Chicago Natural History Museum P26151) do not agree in size with the upper teeth found associated with lowers of *P. francesi* (fig. 13e). Wood's specimens should be referred to *Paramys excavatus*.

*Pseudotomus coloradensis* Wood, 1962

Only a few isolated incisors from the Lost Cabin deposits have been referred to this species. They add nothing to Wood's type description.

*Lophiparamys debequensis* Wood, 1962

Only a few isolated teeth of this species have been recovered from the Lost Cabin deposits. An  $M_3$  (CM 22234, fig. 14b), differs from the only previously known  $M_3$  of this species (AC 2540) in that the entoconid is separated from the posterior cingulum instead of being continuous with it. Other minor differences between the Lost Cabin specimen and previously described material are due to the greater amount of wear on the Lost Cabin specimen.

An isolated  $P_4$  (CM 22235, fig. 14a), is similar to  $P_4$  in *L. murinus* and on the basis of size is referred to *L. debequensis*. The protoconid of this tooth is minute, and the entoconid, although displaced inward from the posterior edge of the tooth, is continuous with the posterior cingulum. A number of isolated incisors from the Lost Cabin are the size of this species or of *Dawsonomys minor*, but seem referable to *Lophiparamys* by shape (table 19).

*Lophiparamys woodi*, new species

TYPE: CM 22241, left  $M_3$ .

HOLOTYPE: Type specimen and CM 22240,  $RM_3$ ; CM 22236-22239, isolated upper molars.

HORIZON AND LOCALITY: Lost Cabin Member, Wind River formation, locality 4.

DIAGNOSIS: A large *Lophiparamys*. Lower molars with entoconid isolated from posterior cingulum, protoconid not connected to anterior cingulum, enamel deeply crenulated. Measurements in table 19. Fig. 14c-e.

DISCUSSION: This species is larger than previously described members of this genus and is a descendant of *L. murinus* of the Gray Bull, the largest previously known species. Only one upper tooth of *Lophiparamys*

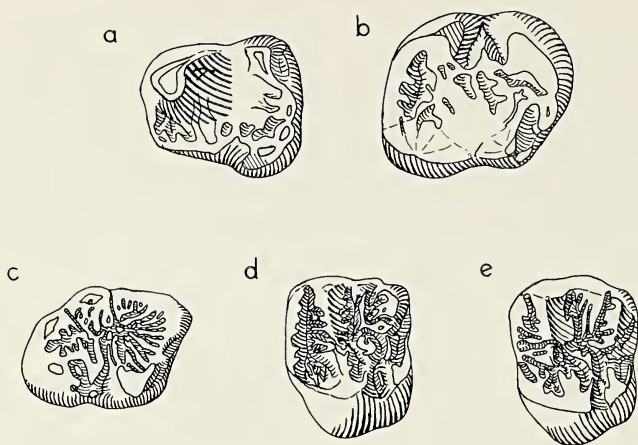


Fig. 14. a-b. *Lophiparamys debequensis*. a. CM 22235, LP<sub>4</sub>. b. CM 22234, RM<sub>3</sub>. c-e. *Lophiparamys woodi*. c. CM 22241, LM<sub>3</sub>, type. d. CM 22236, LM<sup>1</sup>. e. CM 22237, ?LM<sup>2</sup>. All x7.5.

was previously known, an M<sup>3</sup> of *L. debequensis*. Several upper teeth from the Lost Cabin appear to belong to *L. woodi*. These teeth show a well developed hypocone, and an anterior cingulum separated from both the protocone and paracone. Both these features are characteristic of the Microparamyinae, and the amount of crenulation on these teeth clearly place them in *Lophiparamys*.

#### Family Sciuravidae

##### Sciuravid cf. *Dawsonomys minor* Wood, 1965

Two isolated lower molars and a few isolated incisors of a small sciuravid tentatively are referred to this species. The material is so fragmentary and differs enough from the only known specimen of *Dawsonomys minor*, that exact identification is not possible. One lower molar, considered LM<sub>2</sub> (CM 22242, fig. 15b), differs from the type specimen in that the ridge from the metaconid cuts across the trigonid basin instead of passing anterior to it. The anterior cingulum is incomplete, and the entoconid is more directly connected to the hypoconulid than it is in the type. The other specimen, considered LM<sub>1</sub> (CM 22243, fig. 15a), also exhibits separation between the metaconid and anterior cingulum.



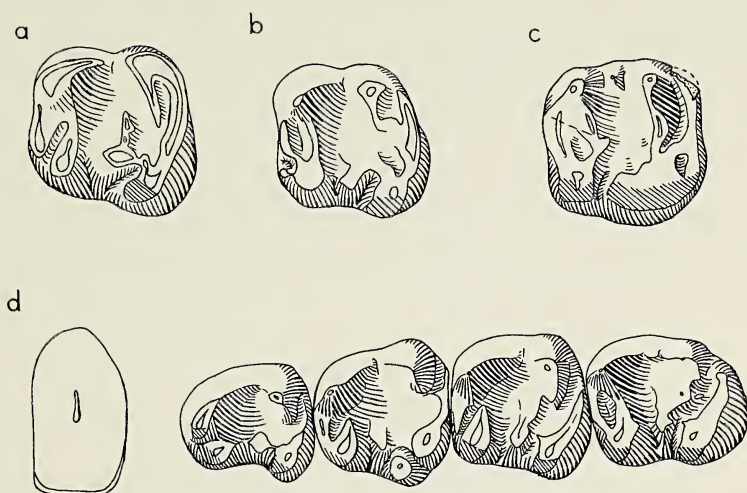


Fig. 15. a-b. Sciuravid, cf. *Dawsonomys minor*. a. CM 22243, LM<sub>1</sub>, x15. b. CM 22242, LM<sub>2</sub>, x15. c-d. *Knightomys depressus*. c. CM 22253, RM<sub>1</sub>, x10. d. CM 22251, LL<sub>1</sub>, P<sub>4</sub>-M<sub>3</sub>, x10.

### *Mysops kalicola* Matthew, 1918

The only known material of this species is the collection of three specimens mentioned by Matthew (1918).

### *Knightomys depressus* (Loomis, 1907)

This species is well represented in the Lost Cabin (table 20). The specimens are similar to the Lysite sample of this species, rather than to *K. senior* of the La Barge fauna, in possessing an accessory mental foramen and an entoconid ridge directed towards the hypoconulid. One specimen, possessing an extra cusp on M<sub>1</sub>, is illustrated in fig. 15d, with the only upper molar of *Knightomys* known from the Lost Cabin (fig. 15c).

Wood (1965: 127) noted that in the Lysite, *Microparamys lysitensis* and *Knightomys depressus* are morphologically congeneric, and that *M. lysitensis* is very probably not congeneric with the genotype of *Microparamys*. After examining specimens referred to these two species from both the Lysite and Lost Cabin deposits, I conclude that only a single species is represented, and consider *M. lysitensis* a synonym of *Knightomys depressus*. The main character used to separate these two species was the greater crest development on the teeth of *Knightomys*,

but all known specimens of *Microparamys lysitensis* are worn, the wear eliminating the crests. I find no differences, other than state of wear, separating these two species. The specimen from the Lost Cabin referred to *Paramys murinus* by White (1952) is a worn *Knightomys* specimen.

The unique type specimen of *Microparamys cathedralis* also appears, from Wood's (1962) illustrations, to be a worn specimen of *Knightomys*. I refer *M. cathedralis* to *Knightomys*. These changes in taxonomy, and those discussed under *Paramys francesi*, remove the genus *Microparamys* from the early Eocene.

#### Order Carnivora

#### Family Miacidae

##### *Didymictis altidens* Cope, 1880

Several specimens of this species, including the type specimen, have been recovered from the Wind River Lost Cabin. Measurements of this sample, and of the Wind River Lysite sample of *D. protenus* (from which *D. altidens* is descended) are presented in table 21.

##### *Viverravus gracilis* Marsh, 1872

The sample (table 22) adds nothing to Robinson's (1966) treatment of this species.

##### *Viverravus lutosus* Gazin, 1952

This species, previously unreported from the Wind River Lost Cabin, is represented by several specimens (CM 21230, 22271-22274) whose measurements are presented in table 22. The Lost Cabin specimens have a longer and narrower  $P_4$  and a shorter  $M_{1-2}$  than Lysite specimens of this species, but these differences are not great enough to merit specific separation.

##### *Miacis latidens* Matthew, 1915

The type specimen (AMNH 14760) and five other specimens (AMNH 14770, USNM 18448, CM 22283, 21189, 21199) are known from the Wind River Lost Cabin. These specimens exhibit a smaller  $M_3$ , slightly larger  $M_2$ , and much larger  $M_1$  than the Lysite sample of this species (compare table 23 with Guthrie, 1967a).

##### *Miacis exiguus* Matthew, 1915

The species, previously unrecorded from the Wind River Lost Cabin, is represented by three jaw fragments (PU 19354 and CM 22281). These

specimens have a single-rooted  $M_3$  instead of a two-rooted one as in the Lysite sample of *M. exiguus*, and  $M_{1-2}$  are distinctly larger than in the Lysite specimens (compare table 23 with Guthrie, 1967a). In these respects the Lost Cabin sample approaches *M. parvivorus* of the Bridger formation.

*Miacis jepseni* Guthrie, 1967

The presence of this species in the Lost Cabin is established by AMNH 14771, a pair of nearly edentulous jaws. This specimen is identified as *Miacis* by the configuration of the jaw and alveoli, and as this species because of its size.

*Oödetes* sp.

According to Dr. Giles MacIntyre, two specimens from the Lost Cabin, AMNH 2970 and an uncatalogued American Museum specimen, are referable to *Oödetes*. The specimens belong to an undescribed species.

*Vulpavus canavus* Matthew, 1915

This is the commonest Lost Cabin carnivore, represented by the remains of well over a dozen individuals, including the type specimen (table 24). Previously (Guthrie, 1967a) I referred the Lysite sample of *Vulpavus* to *V. canavus* and suggested that *V. australis* was a synonym of this species. The latter position was in error. The Lost Cabin sample of *Vulpavus* clearly contains two species, the larger common *V. canavus* and a smaller, rare species, here considered *V. australis*.

The Lost Cabin specimen listed by Matthew (1915a) as *Vassacyon promicrodon* (AMNH 84) is a specimen of *V. canavus*. The Huerfano specimens referred to *V. asius* by Robinson (1966) and the New Fork specimens referred to *V. asius* by Gazin (1962) and to *Vulpavus* sp. by West (1968) also appear to belong to *V. canavus*. The proximity of the metaconid to the paraconid noted in *V. asius* and in Robinson's specimens appear in variants both in *V. australis* and *V. canavus*. This feature is not considered of specific value.

The Lost Cabin sample contains several upper molars. Since the maxilla of *V. canavus* has not been adequately illustrated previously, these, along with a specimen containing  $DP^4$ , are illustrated in fig. 16a-c.

*Vulpavus australis* Matthew, 1915

Only the two specimens referred to this species by Matthew (1915a) have been recovered from the Wind River Lost Cabin deposits (table



24). These specimens, and the American Museum sample of *V. australis* from the Lysite of the Big Horn Basin are nearly identical in size and shape to the type specimen of *V. asius* from the La Barge (Gazin, 1952). Other characteristics, such as the difference in jaw depth that Gazin notes between the type specimens of these species, are not considered valid grounds for their separation since this character varies with age of the individual. *V. asius* is therefore considered a synonym of *Vulpavus australis*, although many of the specimens referred to *V. asius* from other horizons belong to *V. canavus* (see discussion above).

*Uintacyon asodes* Gazin, 1952

This species is represented in the Wind River Cabin by several specimens (table 25) including the first known maxilla of this species (fig. 16d). Compared with *U. massetericus*, *M*<sup>1</sup> is much narrower, and the

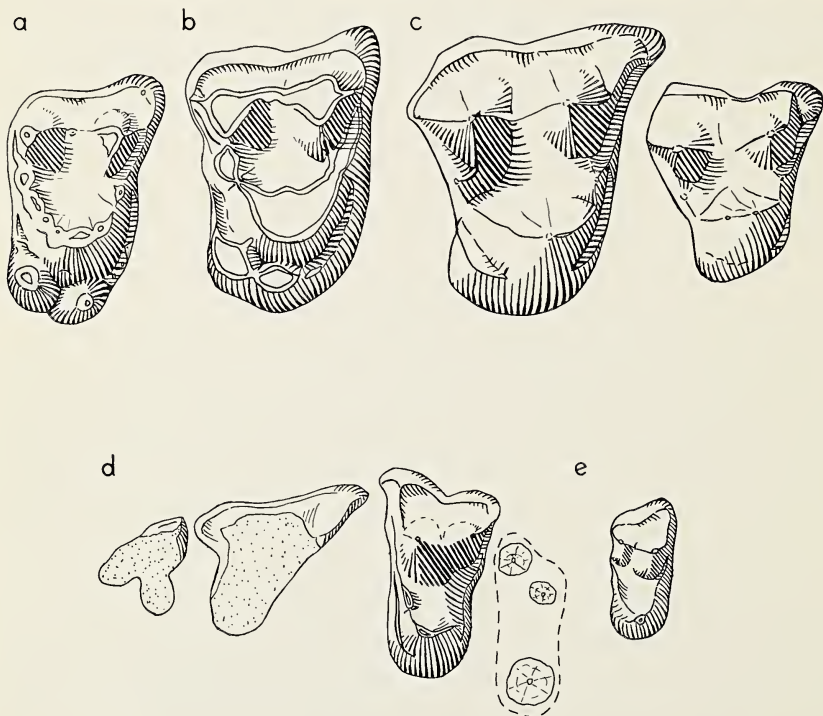


Fig. 16. a-c. *Vulpavus canavus*. a. CM 22287, RM<sup>3</sup>. b. CM 22292, RM<sup>2</sup>. c. PU 19355, RDP<sup>4</sup>, M<sup>1</sup>. x5. d. *Uintacyon asodes*, CM 22295, LP<sup>4</sup>-M<sup>2</sup>, x2.5. e. *Uintacyon massetericus*, CM 22518, RM<sup>3</sup>, x2.5.

paracone and metacone are very close together. As the crowns are broken,  $P^4$  and  $P^3$  are shown only in outline, but  $P^3$  evidently had a protocone. An  $M^2$  of *U. massetericus* from the Lysite, not previously illustrated, is also shown to complete the maxilla.

Order Condylarthra

Family Esthonychidae

*Esthonyx acutidens* Cope, 1881

Measurements of the Lost Cabin sample are presented in table 26.

Family Mesonychidae

*Hapalodectes leptognathus* (Osborn and Wortman, 1892)

The two specimens known from the Lost Cabin (AMNH 14748 and CM 22516), both fragmentary jaws, add nothing to Szalay's (1969b) analysis of this group.

Mesonychid, genus and species indeterminate

An isolated astragalus (AMNH 12791), that could belong to either *Mesonyx* or *Pachyaena*, is the only large mesonychid specimen from the Lost Cabin deposits.

Family Hyopsodontidae

*Hyopsodus wortmani* Osborn, 1902

*Hyopsodus miticulus* (Cope, 1874)

*Hyopsodus walcottianus* Matthew, 1915b

The taxonomy of the Lost Cabin sample of *Hyopsodus* has been adequately treated (Guthrie, 1967a; Gazin, 1968). Only measurements of this sample are presented here (tables 27-29). Although measurements of  $M_3$  from *H. miticulus* and *H. wortmani* overlap, the teeth in question were associated with other lower molars whose identification was possible on the basis of size.

Family Phenacodontidae

The taxonomy of the smaller Lost Cabin species of *Phenacodus*, *P. vortmani*, was discussed earlier (Guthrie, 1967a) and needs no additional comment. The taxonomy of the larger Lost Cabin species of *Phenacodus* is uncertain, and requires further comment.

Both Granger (1915) and Simpson (1937) separated the large specimens of *Phenacodus* from the Gray Bull deposits into four groups. These are *Phenacodus primaevus primaevus*, *P. p. hemiconus*, *P. robustus*

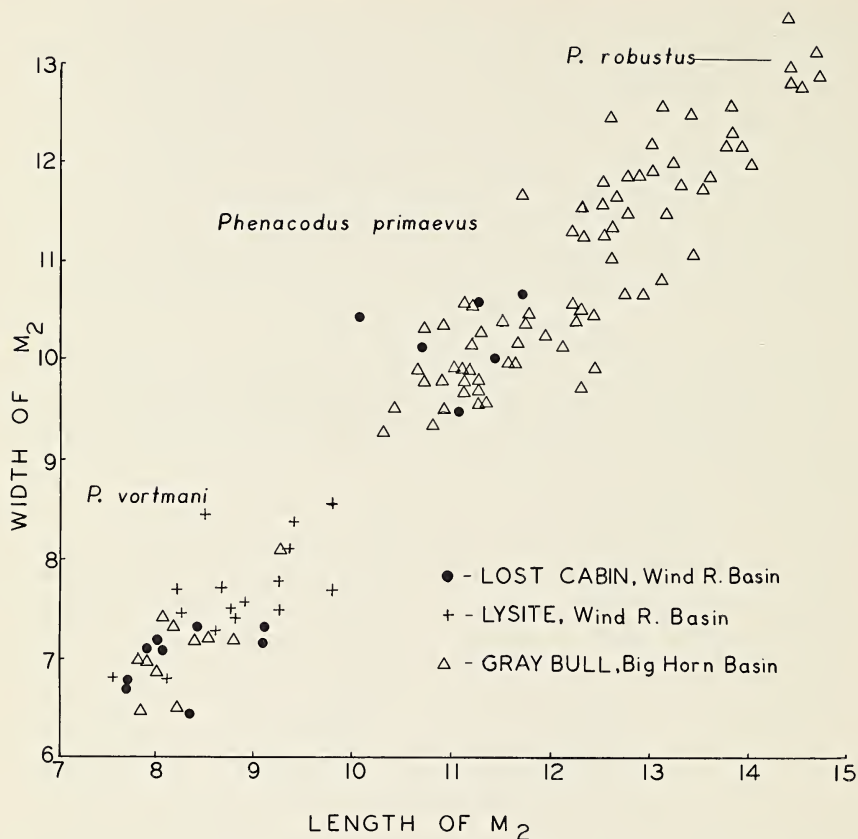


Fig. 17. Measurements of lower  $M_2$  for large *Phenacodus* from the early Eocene.

(considered *P. p. robustus* by Granger) and *P. intermedius* (considered *P. p. intermedius* by Simpson). My examination of all Gray Bull material in the American Museum and the Yale collections shows that this four-fold division is not valid. A threefold division might be valid, for there is a slight separation of the sample into subgroups on the basis of size (fig. 17). However, the total sample (including the species *P. primaevus*, *P. intermedius* and *P. robustus* of previous authors) contains within it a range of variation comparable to that of several other species (coefficient of variation 6-9). Further complications are that specimens of *Phenacodus* in this size range are completely absent from Lysite deposits, and only the smallest end of this size range is present in the



Lost Cabin. I am inclined to consider *P. robustus* a valid species with a narrow range of variation, and to consider *P. intermedius* a synonym of *P. primaevus*. I do not retain the subdivision of *P. primaevus* into subspecies for the reasons stated by Gazin (1956), and noted above in the discussion of the rodent *Paramys copei*.

*Phenacodus primaevus* Cope, 1873

The Lost Cabin sample of this species consists, except for one large specimen (AMNH 14786, a maxilla), of specimens in the size range of *P. intermedius* of authors (table 30).

*Phenacodus vortmani* (Cope, 1880)

The taxonomy of this species was discussed previously (Guthrie, 1967a), and measurements of the Lost Cabin sample are presented in table 31.

*Ectocion superstes* is based on a single specimen (AMNH 233a) from an unknown Lost Cabin locality. As I can barely distinguish this specimen from specimens of *Phenacodus vortmani*, I regard it as a slightly aberrant individual of the latter species, as McKenna suggested (1960a). It differs from typical *P. vortmani* only in the possession of a well-developed entoconid on P<sub>4</sub> and a prominent heel on P<sub>3</sub>. However, both these features are present in several members of the Lost Cabin sample of *P. vortmani*.

Family Meniscotheriidae

*Meniscotherium chamense* Cope, 1881

Nothing can be added to Gazin's (1965) review of this species.

Order Pantodonta

Family Coryphodontidae

*Coryphodon* cf. *C. radians* (Cope, 1872)

About twelve specimens of *Coryphodon* are known from the Wind River Lost Cabin. All seem referable to a single species, probably *C. radians*. Identification can only be tentative until this genus is revised.

Order Dinocerata

Family Uintatheriidae

*Bathyopsis fissidens* Cope, 1881

The type specimen of this species (AMNH 4820) and a few other excellent specimens including a skull (AMNH 14802), have been re-

covered from the Wind River Lost Cabin. These specimens, which have unworn teeth, look quite different from the only known specimen of *Probathyopsis lysitensis*, which has very worn teeth. New material of *Bathyopsis*, worn to the state found in the type specimen of *Probathyopsis*, indicates that the teeth of these species are identical in size and nearly identical in configuration. The presence of the hypoconulid crest in *Probathyopsis* and not in *Bathyopsis* is the only difference between the two species.

### Order Perissodactyla

#### Family Equidae

*Hyracotherium vasacciense* (Cope, 1872)

*Hyracotherium craspedotum* Cope, 1880

*Hyracotherium index* (Cope, 1873)

The Wind River Lost Cabin fauna contains three species of *Hyracotherium*. A rare small species, *H. index* (table 33), was not recognized by Kitts (1956) but has been reported from both Lysite (Guthrie, 1967a) and La Barge (Gazin, 1952) deposits. The specimens on which this species is based might represent extremely small variants of *H. vasacciense*, but are separable from this species on the basis of size. Measurements presented here for *H. vasacciense* (table 32) differ from those of Kitts (1956; table 15) since his sample included specimens here referred to *H. craspedotum* (AMNH 14817, 14838). An important result of this change is that *H. vasacciense*, previously thought to increase in mean size between the Lysite and Lost Cabin horizons, is now shown to decrease in size during this period, reversing the trend in this species during the Lysite (Guthrie, 1967a). The relationships that I suggested between lineages of *Orohippus* and *Hyracotherium* (Guthrie, 1967a), based on the assumption that *H. vasacciense* increased in size during the Lostcabinian, are wrong, and Kitt's (1957) view of the relationship between these genera is correct. *Hyracotherium vasacciense* gave rise to the smaller *O. pumilus*, and *H. craspedotum* produced the smaller *O. major*.

#### Family Brontotheriidae

*Lambdotherium popoagicum* (Cope, 1880)

Measurements of the complete sample from the maroon shale layer and its equivalents are presented in table 34.

*Eotitanops borealis* (Cope, 1880)

Robinson (1966) considered the Lost Cabin sample from the Wind River Basin to include a single species. Although the variation in this sample is large (table 35), I agree, at least until more material is recovered.

## Family Isectolophidae

*Homogalax protapirinus* (Wortman, 1896)

The first Wind River Lost Cabin specimens referable to this genus are a few isolated teeth (CM 22389-22390, fig. 18a, b). Although these specimens fall at the lower end of the size range for the Gray Bull

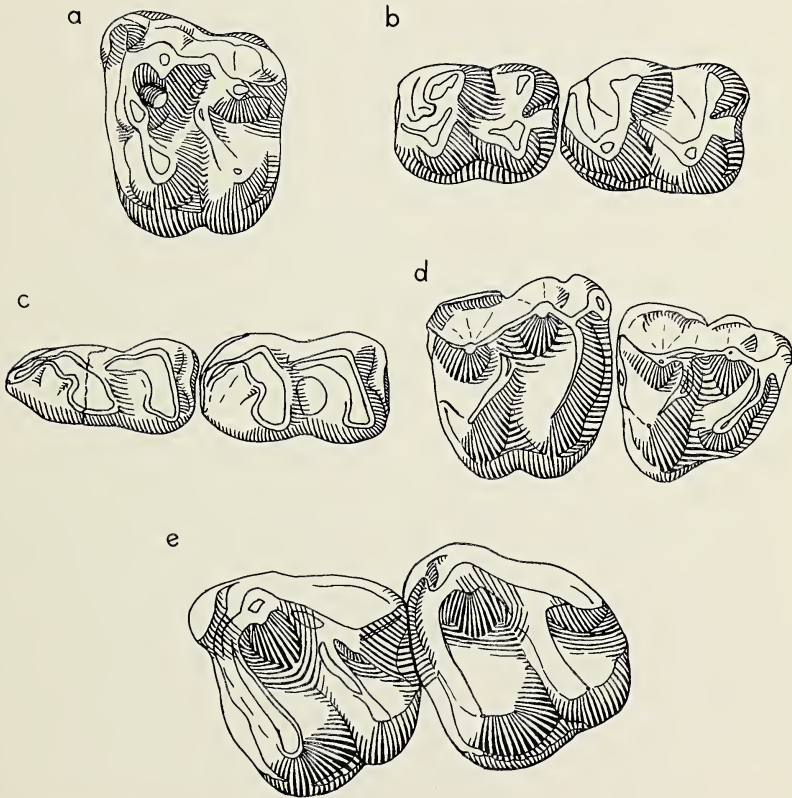


Fig. 18. a-b. *Homogalax protapirinus*. a. CM 22384, LM<sup>2</sup>. b. CM 22390, RM<sub>1</sub>-M<sub>2</sub>, x2.5. c-e. *Selenalestes scopaeus*. c. CM 22391, RDP<sub>3</sub>-DP<sub>4</sub>. d. CM 21125, LM<sup>2</sup>-M<sup>3</sup>. e. CM 22391, RDP<sup>3</sup>-DP<sup>4</sup>, x4.



sample of this species, they agree with small specimens of Lostcabinian age from Dad, Wyoming, reported by Gazin (1962) and referred to this species by Radinsky (1963).

An isolated  $M_2$  (CM 22517), referable to *Homogalax* and from the Lysite deposits of the Wind River Basin, is the first Wind River Lysite record of this genus.

### Family Helaletidae

#### *Selenaletes scopaeus* Radinsky, 1966

Four additional specimens of this species have been recovered since its description. One of these, a jaw with  $LM_{1-2}$  (CM 22392), is similar in all respects to earlier described material. A second specimen, CM 22391 (fig. 18b), appears to consist of  $RDP_{3-4}$  and compares favorably with known milk teeth of *Chasmotherium* (Butler, 1952). The two other specimens, one a portion of a right maxilla with  $DP^{3-4}$  (CM 22391, fig. 18d), the other a left maxilla with  $M^{2-3}$  (CM 21125, fig. 18e), are the first upper teeth of this species that have been recovered.

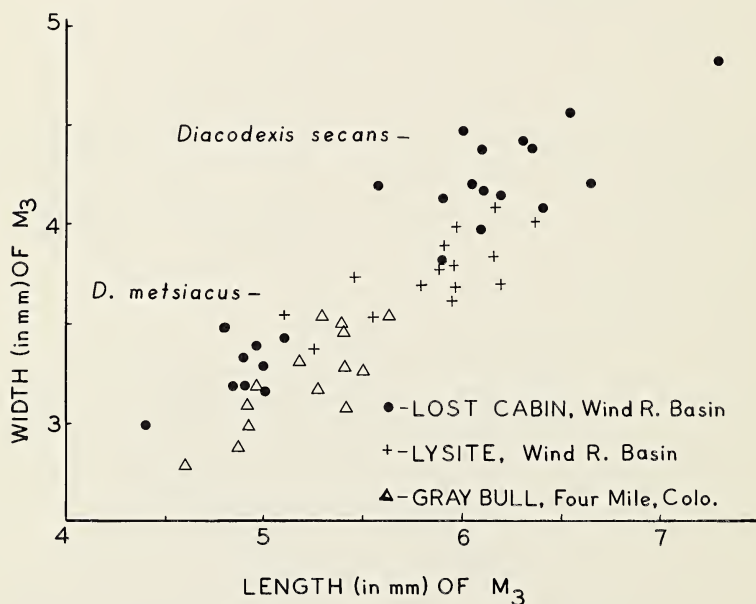


Fig. 19. Measurements of  $M_3$  for early Eocene *Diacodexis*.

*Heptodon calciculus* (Cope, 1880)

*Heptodon posticus* (Cope, 1882)

The new material of these species adds nothing to Radinsky's (1963) treatment.

*Hyrachyus modestus* (Leidy, 1870)

To the two specimens previously known (AMNH 14887, 4887, Wood, 1934) can be added CM 22439, an isolated M<sub>2</sub> measuring 18.0 mm. in length and 12.10 mm. in width.

Order Artiodactyla

Family Dichobunidae

*Diacodexis metsiacus* (Cope, 1882)

*Diacodexis secans* (Cope, 1881)

The Lost Cabin fauna contains two species of *Diacodexis*. The larger species is characterized by greater width of the lower molars (table 37, figs. 19, 20b, c) and includes the type specimens of *D. olseni* and *D. secans*. Sinclair (1914) suggested, and several authors since have agreed, that *D. secans*, although advanced and atypical in the absence of a paraconid on M<sub>2</sub>, resembles the rest of the Lost Cabin sample of *Diacodexis olseni* in all other ways, and has priority over this latter name.

The smaller species (table 36, figs. 19, 20a) is nearly identical to the Four Mile sample of *D. metsiacus* in size and is clearly smaller than the sample of this species from the Lysite deposits. This small species, previously unrecognized in the Lost Cabin, is derivable from the Lysite sample of *D. metsiacus* and is referred there despite its slightly smaller size. The reversal in trend towards increase in size that *D. metsiacus* shows from the Four Mile horizon to the Lysite is probably due to competition with *D. secans* in the Lostcabinian period.

The specimen referred to *D. chacensis* by Robinson (1966) seems better assigned to *D. metsiacus*. Gazin (1952) pointed out that the type of *D. chacensis* is very large, and until a larger sample of the New Mexican species is obtained and its age determined, the name should not be applied to the smaller Wyoming forms.

*Antiacodon* Cope, 1872

The genus *Antiacodon* was shown by Gazin (1955) to be based upon *A. pygmaeus*. *Sarcolemur furcatus* was referred to *Antiacodon* by Cope

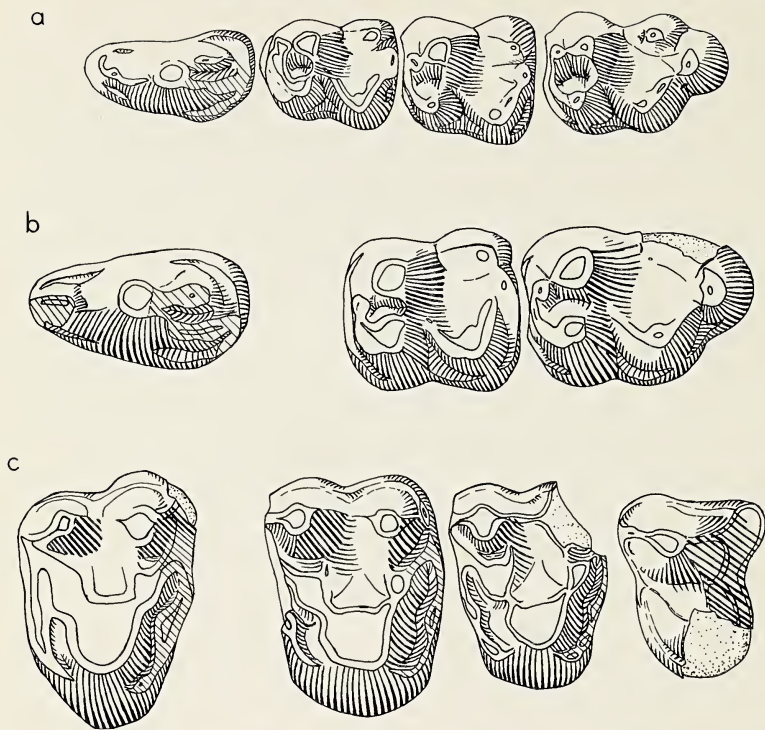


Fig. 20. a. *Diacodexis metsiacus*, CM 22512, LP<sub>4</sub>-M<sub>3</sub>. b-c. *Diacodexis secans*. b. Composite of CM 22503, LP<sub>4</sub>, and CM 21135, LM<sub>2</sub>-M<sub>3</sub>. c. Composite of CM 22507, RP<sub>4</sub>-M<sub>2</sub>, and CM 22508, RM<sub>3</sub>. All x5.

and later considered a synonym of *A. pygmaeus*. These two species, although their teeth are similar in size and in most morphological features, and although they are from the same deposits, do differ in the following characteristics.

*Antiacodon (A. pygmaeus)*

P<sub>4</sub> simple, lacking internal cusp.

Hypoconulid on M<sub>1-2</sub> connected to the entoconid and hypoconid by a ridge along the posterior margin of the tooth.

*Sarcolemur (S. furcatus)*

P<sub>4</sub> complex, elongate, with prominent internal cusp.

Hypoconulid on M<sub>1-2</sub> isolated at the posterior margin of the tooth, the entoconid and hypoconid connected directly by a ridge.

These differences, pointed out by Osborn (1902), are considered valid specific characters and not individual variations as must be the case if *Sarcolemur furcatus* is included in *Antiacodon pygmaeus*. Furthermore, these differences are considered of generic value since the two species



are members of lineages differing in origin and evolutionary history. The genus *Antiacodon* can be traced, through *A. vanvaleni*, to an origin in the Gray Bull from a form near *Diacodexis robustus*. *Sarcolemur* is descended from *Hexacodus* (a synonym of *Sarcolemur*), the genus first appearing in the La Barge. Lostcabinian specimens of *Sarcolemur* (*Hexacodus*) are less advanced than contemporary specimens of *Antiacodon* in the development of lophs on the lower molars, and are restricted in range to southern Wyoming, while *Antiacodon* is found in association with *Diacodexis* in the Wind River Basin where *Sarcolemur* is absent.

The separation of *Antiacodon* from *Sarcolemur* invalidates Gazin's (1955) characterization of *Antiacodon*, which was based in part on the characters here assigned to *Sarcolemur*. Gazin is right, however, in considering *Sarcolemur* (*Hexacodus*) the ancestor of most of the Bridgerian artiodactyls. *Sarcolemur* is also very close to the European *Protodichobune*, which also might be considered a synonym of *Sarcolemur*.

### ***Antiacodon vanvaleni*, new species**

TYPE: CM 22513, a jaw fragment with RM<sub>1-2</sub>.

HYPODIGM: Type specimen and CM 22514, 21007, 21009, 21014, 21024, 20998, PU 18399, all lower jaw fragments.

HORIZON AND LOCALITY: Lost Cabin Member of the Wind River formation, locality 1.

DIAGNOSIS: Hypoconulid and entoconid rounded, not cuspsate as in *A. pygmaeus*; paraconid smaller than metaconid (often larger in *A. pygmaeus*). Measurements in table 38; fig. 21a, b.

DISCUSSION: This species can be separated from contemporary *Diacodexis* by the development of lophs on the lower molars (compare figs. 20, 21), and from *Sarcolemur* by the configuration of the talonid, especially the relationship of the hypoconulid to the other cusps. A likely ancestor of *A. vanvaleni* is found in some specimens from the Gray Bull deposits referred to *Diacodexis robustus*. These specimens (AMNH 15513, 2852) do not have the pattern of rounded, unconnected cusps on the trigonid of the lower molars that is found in the type specimen of *D. robustus* (compare fig. 21c with fig. 21d), but instead show the development of a paralophid and protolophid in a less advanced form than is shown in *A. vanvaleni*. These Gray Bull specimens also have the hypoconulid in a more central position between the hypoconid and entoconid than do the Lost Cabin specimens of *A. vanvaleni*, where the hypoconulid is shifted towards the entoconid as it is in *A. pygmaeus*. Although much variation exists among Gray Bull specimens of *Dia-*

*codexis robustus* I have not divided this sample into two species as it is not clear that at this early stage the variation shown is not within a single species.

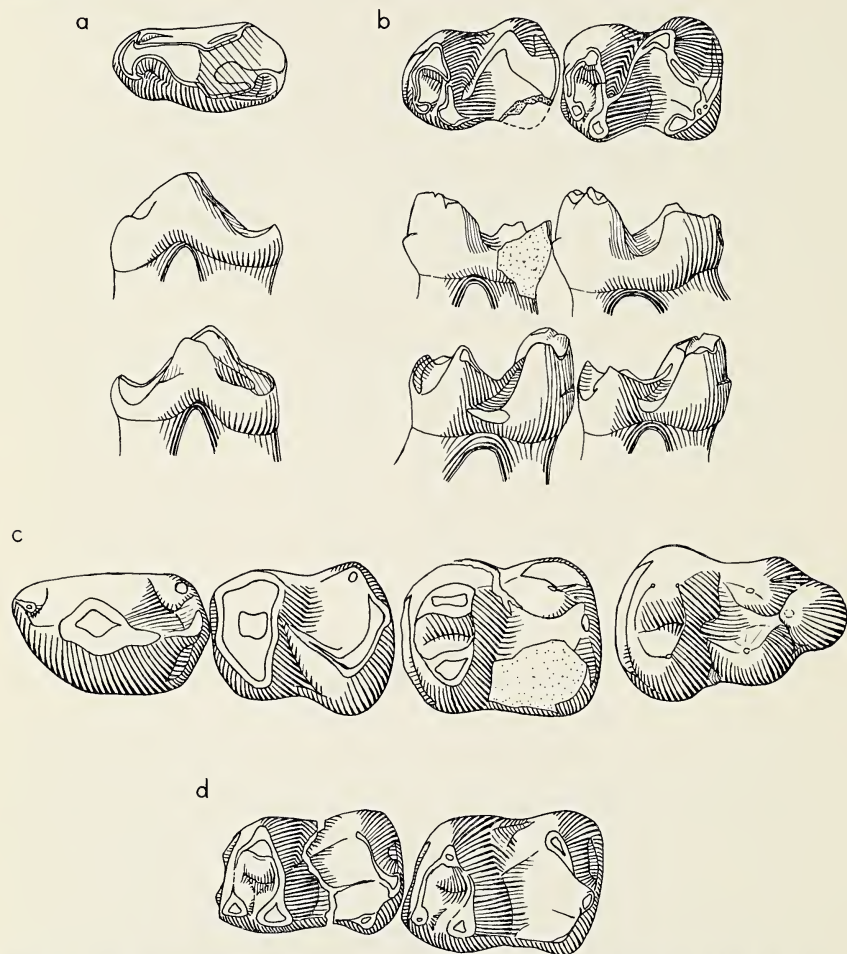


Fig. 21. a-b. *Antiacodon vanvaleni*. a. CM 22514, LP<sub>4</sub>. b. CM 22513, RM<sub>1</sub>-M<sub>2</sub>, type. c-d. *Diacodexis robustus*. c. Composite of AMNH 15512, RP<sub>4</sub>-M<sub>1</sub> reversed, and AMNH 15514, LM<sub>2</sub>-M<sub>3</sub>, type. d. AMNH 15513, RM<sub>1</sub>-M<sub>2</sub>. All x4.5.

### *Bunophorus* Sinclair, 1914

Three species of *Bunophorus* have been described: the small species *B. macropterus*, which is restricted for the most part to the Lysite horizon, and two larger species, *B. etsagicus* and *B. sinclairi*. These

latter species are identical in size and are most common in Lost Cabin deposits, although a few specimens are known from Lysite deposits. The type specimen of *B. etsagicus* lacks a deuterocoenid (paraconid) on  $P_4$  and has a *crista obliqua* on the lower molars. It is similar to *B. macropternus* in both these characters. I described specimens identical to *B. etsagicus* in size as a new species, *B. sinclairi* (Guthrie, 1966) since these specimens possessed a well-developed deuterocoenid on  $P_4$  and lacked a *crista obliqua*. It now appears that nearly all the specimens of *Bunophorus* from Lost Cabin horizons are similar to *B. sinclairi* in morphology. The type of *B. etsagicus* was collected by Wortman in 1881 in the Big Horn Basin and is probably Lysitean in age. I now consider *B. sinclairi* a synonym of *B. etsagicus*, the type specimen of *B. etsagicus* being an atypical primitive variant within this species that has not yet lost the *crista obliqua* on the lower molars or gained a deuterocoenid on  $P_4$ .

*Bunophorus etsagicus* (Cope, 1882)

This species is well represented in the Lost Cabin deposits (table 39). Upper molars that seem definitely from this species are illustrated in fig. 22a. The sample of *Bunophorus* from the Huerfano facies referred to cf.

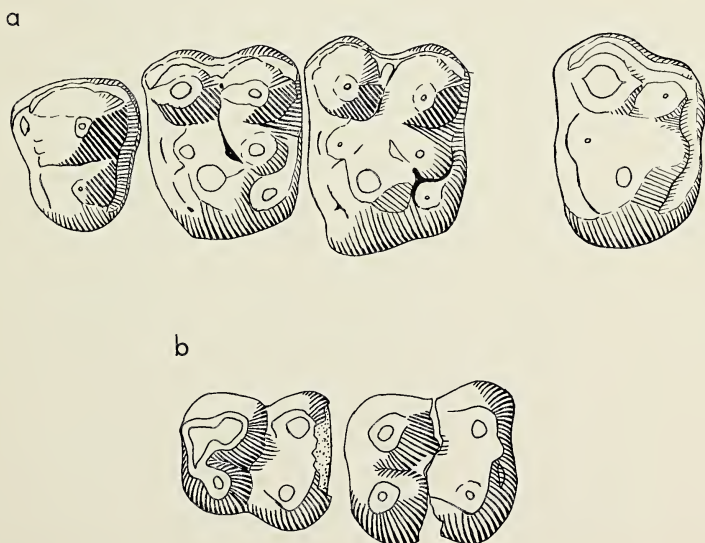


Fig. 22. a. *Bunophorus etsagicus*, composite of AMNH 14940,  $LP^4$ - $M^2$ , and AMNH 14789,  $LM^3$ , x3. b. *Bunophorus gazini*, CM 22483,  $LM_1$ - $M_2$ , type, x2.5.



*B. macropternus* by Robinson (1966) agrees in size with *B. etsagicus*, and should be referred to this species.

***Bunophorus gazini*, new species**

TYPE: CM 22483, a jaw fragment with  $M_{1-2}$ .

HYPODIGM: Type specimen only.

HORIZON AND LOCALITY: Lost Cabin Member of the Wind River formation, locality 1.

DIAGNOSIS: A large *Bunophorus*, exhibiting all the characteristics of *B. etsagicus* but distinctly larger; length and width measurements for  $M_2$  are 9.00 mm. x 8.30 mm. and for  $M_1$  8.10 mm. x 7.20 mm.; figure 22b.

DISCUSSION: The three species of *Bunophorus* now known are nearly contemporaneous, distinguishable from one another by size, and not easily derivable from one another or from any other early Eocene artiodactyl.

TABLE 1

FAUNAL LIST FOR THE LOST CABIN MEMBER OF THE WIND RIVER FORMATION

	Minimum number of individuals	Per cent of total fauna
Marsupialia	3	.32
<i>Peratherium</i> cf. <i>P. chesteri</i>	2	.22
<i>Peratherium comstocki</i>	1	.10
Insectivora	45	4.84
<i>Palaeictops bicuspis</i>	10	1.08
<i>Palaeictops multicuspis</i>	2	.22
<i>Apatemys whitakeri</i>	5	.54
<i>Apatemys</i> cf. <i>A. bellus</i>	1	.10
<i>Entomolestes nitens</i>	2	.22
<i>Myolestes dasypelix</i>	3	.32
<i>Talpavus sullivanii</i>	3	.32
<i>Palaeosinopa didelphoides</i>	16	1.72
<i>Palaeosinopa lutreola</i>	2	.22
<i>Palaeosinopa</i> cf. <i>P. veterrima</i>	1	.10
Deltatheridia	38	4.10
<i>Didelphodus altidens</i>	5	.54
<i>Patriofelis tigrinus</i>	5	.54
<i>Prolimnocyon antiquus</i>	6	.65
<i>Paeneprolimnocyon amissadomus</i>	6	.65
<i>Prototomus multicuspis</i>	5	.54
<i>Tritemnodon strenua</i>	11	1.18
Primates	174	18.71
<i>Notharctus nunienus</i>	36	3.88
<i>Notharctus venticolus</i>	47	5.06
<i>Shoshonius cooperi</i>	27	2.91
<i>Loveina zephyri</i>	3	.32
<i>Absarokius noctivagus</i>	7	.75
<i>Phenacolemur citatus</i>	3	.32
<i>Phenacolemur jepseni</i>	1	.10
<i>Microsypops scottianus</i>	45	4.84
<i>Microsypops lundeliusi</i>	4	.43
<i>Microsypops latidens</i>	1	.10
Taeniodonta	5	.54
<i>Stylinodon cylindrifera</i>	5	.54
Edentata	6	.65
<i>Palaeonodon ignavus</i>	4	.43
<i>Tubulodon taylori</i>	2	.22
Rodentia	156	16.80
<i>Paramys copei</i>	75	8.07
<i>Paramys excavatus</i>	20	2.15
<i>Paramys francesi</i>	20	2.15
<i>Thisbomys perditus</i>	9	.97

(TABLE 1, *continued*)

	Minimum number of individuals	Per cent of total fauna
<i>Pseudotomus coloradensis</i>	2	.22
<i>Lophiparamys debequensis</i>	6	.65
<i>Lophiparamys woodi</i>	2	.22
scuravid cf. <i>Dawsonomys minor</i>	2	.22
<i>Mysops kalicola</i>	3	.32
<i>Knightomys depressus</i>	17	1.83
Carnivora	60	6.46
<i>Didymictis altidens</i>	10	1.08
<i>Viverravus gracilis</i>	15	1.61
<i>Viverravus lutosus</i>	5	.54
<i>Miacis latidens</i>	6	.65
<i>Miacis exiguus</i>	3	.32
<i>Miacis jepseni</i>	1	.10
<i>Oidectes</i> sp.	2	.22
<i>Vulpavus canavus</i>	13	1.40
<i>Vulpavus australis</i>	2	.22
<i>Uintacyon asodes</i>	3	.32
Condylarthra	169	18.19
<i>Esthonyx acutidens</i>	14	1.51
<i>Hapalodectes leptognathus</i>	2	.22
Mesonychid, gen. and sp. indet.	1	.10
<i>Hyopsodus wortmani</i>	34	3.66
<i>Hyopsodus miticulus</i>	75	8.07
<i>Hyopsodus walcottianus</i>	6	.65
<i>Phenacodus primaevus</i>	16	1.72
<i>Phenacodus vortmani</i>	16	1.72
<i>Meniscotherium chamense</i>	5	.54
Pantodonta	13	1.40
<i>Coryphodon</i> cf. <i>C. radians</i>	13	1.40
Dinocerata	6	.65
<i>Bathyopsis fissidens</i>	6	.65
Perissodactyla	199	21.43
<i>Hyracotherium vasacciense</i>	49	5.27
<i>Hyracotherium craspedotum</i>	8	.86
<i>Hyracotherium index</i>	2	.22
<i>Lambdotherium popoagicum</i>	70	7.54
<i>Eotitanops borealis</i>	13	1.40
<i>Homogalax protapirinus</i>	2	.22
<i>Selenaletes scopaeus</i>	3	.32
<i>Heptodon calciculus</i>	44	4.47
<i>Heptodon posticus</i>	5	.54
<i>Hyrachyus modestus</i>	3	.32



(TABLE 1, *continued*)

	Minimum number of individuals	Per cent of total fauna
Artiodactyla	55	5.91
<i>Diacodexis metsiacus</i>	12	1.29
<i>Diacodexis secans</i>	19	2.05
<i>Antiacodon vanvaleni</i>	7	.75
<i>Bunophorus etsygicus</i>	16	1.72
<i>Bunophorus gazini</i>	1	.10
	<u>929</u>	<u>100.00</u>

TABLE 2  
MEASUREMENTS (IN MM.) OF *Palaeictops*

<i>P. bicuspis</i>			<i>P. multicuspis</i> AMNH 14741 Type		
	N	O.R.	M	L	R
P <sup>3</sup> L	3	3.40-4.20	3.75	—	—
W	3	2.50-2.80	2.68	—	—
P <sup>4</sup> L	2	3.10-3.50	3.30	—	—
W	3	3.55-3.85	3.67	—	—
M <sup>1</sup> L	4	3.00-3.40	3.16	—	—
W	4	3.70-4.10	3.89	—	—
M <sup>2</sup> L	3	2.45-3.00	2.80	—	—
W	3	4.00-4.50	4.28	—	—
M <sup>3</sup> L	2	2.25-2.50	2.37	—	—
W	1	—	4.00	—	—
P <sub>3</sub> L	2	3.60-3.90	3.75	4.60	4.55
W	2	1.45-1.60	1.53	1.70	1.80
P <sub>4</sub> L	6	3.55-4.10	3.86	4.20	4.30
W	6	1.65-2.00	1.90	2.25	2.30
M <sub>1</sub> L	4	3.00-3.25	3.09	3.00	—
W	5	2.00-2.60	2.29	2.50	—
M <sub>2</sub> L	8	2.75-3.30	3.00	3.20	3.10
W	7	2.00-2.60	2.30	2.55	2.50
M <sub>3</sub> L	2	3.20-3.30	3.25	3.40	3.60
W	4	2.05-2.30	2.18	2.40	2.25

TABLE 3  
MEASUREMENTS (IN MM.) OF *Apatemys whitakeri*

	N	O.R.	M
M <sub>1</sub> L	2	1.70-1.95	1.83
W	1	1.30	1.30
M <sub>2</sub> L	4	1.70-2.10	1.96
W	3	1.30-1.50	1.41
M <sub>3</sub> L	3	2.00-2.30	2.17
W	2	1.40-1.45	1.43

TABLE 4  
MEASUREMENTS (IN MM.) OF *Myolestes dasypelix*

	CM 22016	CM 22017	CM 22018
M <sub>2</sub> L	—	—	1.60a
W tal	—	—	1.00a
W tri	—	—	—
M <sub>3</sub> L	1.20	—	1.40
W tal	0.70	—	0.80
W tri	0.90a	—	0.95a
Depth of jaw below M <sub>2</sub>	2.20	2.50	—

TABLE 5  
MEASUREMENTS (IN MM.) OF *Talpavus sullivanii*

	Lysite AC 2666 Type	CM 22021	Lost Cabin CM 22020	CM 22019	CM 22022
M <sup>1</sup> L	—	—	2.00	—	—
W	—	—	2.60	—	—
M <sup>2</sup> L	—	—	—	2.10a	—
W	—	—	—	2.80	—
M <sub>1</sub> L	—	—	—	—	1.80
W tal	—	—	—	—	1.22
W tri	—	—	—	—	1.15
M <sub>2</sub> L	1.92	—	—	—	—
W tal	1.30	—	—	—	—
W tri	1.22	—	—	—	—
M <sub>3</sub> L	1.88	1.90	—	—	—
W tal	1.10	1.10	—	—	—
W tri	1.03	1.22	—	—	—

TABLE 6  
MEASUREMENTS (IN MM.) OF *Palaeosinopa*

		<i>P. didelphoides</i>			<i>P. lutreola</i>		
		N	O.R.	M	N	O.R.	M
P <sup>4</sup>	L	1	4.20	4.20	—	—	—
	W	1	5.00	5.00	—	—	—
M <sup>1</sup>	L	2	5.00-5.30	5.15	—	—	—
	W	2	6.00-6.40	6.20	—	—	—
M <sup>2</sup>	L	5	4.68-5.20	4.97	—	—	—
	W	5	6.65-7.60	7.05	—	—	—
M <sup>3</sup>	L	—	—	—	—	—	—
	W	—	—	—	—	—	—
P <sub>4</sub>	L	1	5.20	5.20	—	—	—
	W	1	2.70	2.70	—	—	—
M <sub>1</sub>	L	8	5.00-5.30	5.11	2	4.70-4.80	4.75
	W	9	3.35-3.90	3.64	2	3.00-3.15	3.08
M <sub>2</sub>	L	12	5.10-5.60	5.34	—	—	—
	W	12	3.55-4.40	3.91	—	—	—
M <sub>3</sub>	L	4	5.20-5.82	5.58	1	4.75	4.75
	W	4	3.15-3.75	3.51	1	3.12	3.12

TABLE 7  
MEASUREMENTS (IN MM.) OF *Prolimnocyon antiquus*

		N	O.R.	M
P <sup>4</sup>	L	1	6.70	6.70
	W	1	5.25	5.25
M <sup>1</sup>	L	1	6.65	6.65
	W	1	6.70	6.70
M <sup>2</sup>	L	1	4.40	4.40
	W	1	7.80	7.80
P <sub>4</sub>	L	2	5.83-6.75	6.29
	W	2	2.97-3.30	3.14
M <sub>1</sub>	L	3	5.87-6.75	6.27
	W	2	3.30-3.60	3.45
M <sub>2</sub>	L	3	6.60-6.90	6.73
	W	2	3.70-3.85	3.78
M <sub>3</sub>	L	1	1.90	1.90
	W	1	1.55	1.55



TABLE 8  
MEASUREMENTS (IN MM.) OF *Paeneprolimnocyon amissadomis*

		N	O.R.	M
P <sub>2</sub>	L	2	3.00-3.08	3.04
	W	2	1.72-1.80	1.76
P <sub>3</sub>	L	1	3.20	3.20
	W	1	1.90	1.90
P <sub>4</sub>	L	4	3.72-3.82	3.79
	W	4	2.25-2.45	2.35
M <sub>1</sub>	L	4	4.10-4.35	4.21
	W	4	2.65-3.10	2.93
M <sub>2</sub>	L	3	3.32-3.80	3.57
	W	3	2.45-2.72	2.57
M <sub>3</sub>	L	4	2.65-2.80	2.74
	W	4	2.00-2.20	2.11

TABLE 9  
MEASUREMENTS (IN MM.) OF *Notharctus numenius*

		N	O.R.	M	s	V
P <sup>4</sup>	L	4	3.30-3.40	3.34	—	—
	W	4	4.28-4.80	4.53	—	—
M <sup>1</sup>	L	7	3.90-4.40	4.15	—	—
	W	7	5.35-5.95	5.57	—	—
M <sup>2</sup>	L	6	4.35-4.80	4.53	—	—
	W	6	6.00-6.90	6.37	—	—
M <sup>3</sup>	L	12	3.45-4.45	4.07	—	—
	W	12	5.00-6.40	5.80	—	—
P <sub>3</sub>	L	4	2.50-3.60	3.01	—	—
	W	4	1.83-2.30	2.06	—	—
P <sub>4</sub>	L	16	3.40-4.25	3.79±0.05	0.20±0.04	5.28±0.93
	W	16	2.40-3.30	2.66±0.07	0.26±0.05	9.94±1.76
M <sub>1</sub>	L	32	3.85-4.80	4.29±0.04	0.22±0.03	5.21±0.66
	W	32	3.00-3.95	3.43±0.04	0.20±0.03	5.84±0.73
M <sub>2</sub>	L	31	4.00-5.20	4.44±0.04	0.24±0.03	5.51±0.70
	W	31	3.40-4.34	3.74±0.04	0.22±0.03	5.98±0.76
M <sub>3</sub>	L	21	4.88-6.40	5.72±0.10	0.46±0.07	8.09±1.25
	W	17	3.00-4.22	3.54±0.08	0.36±0.06	10.18±1.75

TABLE 10  
MEASUREMENTS (IN MM.) OF *Notharctus venticolus*

		N	O.R.	M	s	V
P <sup>3</sup>	L	2	4.50-4.60	4.55	—	—
	W	2	4.80-4.90	4.85	—	—
P <sup>4</sup>	L	4	4.00-4.80	4.49	—	—
	W	4	5.50-6.40	5.90	—	—
M <sup>1</sup>	L	7	5.15-6.00	5.66	—	—
	W	7	6.62-7.50	6.23	—	—
M <sup>2</sup>	L	11	5.15-6.40	5.78±0.11	0.36±0.08	6.23±1.33
	W	11	7.45-8.30	7.96±0.09	0.30±0.06	3.77±0.80
M <sup>3</sup>	L	11	4.70-5.35	4.98±0.07	0.22±0.05	4.49±0.96
	W	11	6.10-6.90	6.52±0.09	0.28±0.06	4.34±0.92
P <sub>3</sub>	L	5	4.05-4.60	4.34	—	—
	W	5	2.80-3.05	2.93	—	—
P <sub>4</sub>	L	17	4.15-4.95	4.66±0.07	0.30±0.08	6.44±1.61
	W	16	3.00-3.90	3.43±0.06	0.26±0.07	7.72±1.93
M <sub>1</sub>	L	35	4.22-6.00	5.40±0.06	0.35±0.04	6.42±0.77
	W	34	3.85-4.92	4.37±0.05	0.30±0.04	6.87±0.83
M <sub>2</sub>	L	32	4.90-6.20	5.69±0.06	0.35±0.04	6.09±0.76
	W	33	4.20-5.72	4.84±0.06	0.32±0.04	6.53±0.80
M <sub>3</sub>	L	27	6.30-7.80	7.11±0.07	0.39±0.05	5.45±0.74
	W	27	3.85-4.65	4.26±0.04	0.22±0.03	5.25±0.71

TABLE 11  
MEASUREMENTS (IN MM.) OF *Shoshonius cooperi*

		N	O.R.	M	s	V
P <sup>3</sup>	L	2	1.78-1.90	1.84	—	—
	W	2	2.00-2.32	2.16	—	—
P <sup>4</sup>	L	2	1.75-1.82	1.79	—	—
	W	2	1.60-2.55	2.08	—	—
M <sup>1</sup>	L	2	2.00-2.12	2.06	—	—
	W	2	2.95	2.95	—	—
M <sup>2</sup>	L	5	1.90-2.12	2.02	—	—
	W	3	3.10-3.38	3.28	—	—
M <sup>3</sup>	L	3	1.80-2.00	1.91	—	—
	W	3	2.43-3.05	2.84	—	—
P <sub>3</sub>	L	1	1.54	1.54	—	—
	W	1	1.40	1.40	—	—
P <sub>4</sub>	L	6	1.75-1.90	1.84	—	—
	W	6	1.52-1.70	1.55	—	—
M <sub>1</sub>	L	20	2.10-2.40	2.21±0.02	0.09±0.01	4.22±0.67
	W	20	1.68-1.95	1.77±0.02	0.09±0.01	4.89±0.77
M <sub>2</sub>	L	21	2.04-2.30	2.19±0.01	0.06±0.01	2.96±0.46
	W	21	1.72-2.00	1.84±0.02	0.08±0.01	4.35±0.67
M <sub>3</sub>	L	13	2.60-2.95	2.80±0.03	0.10±0.02	3.59±0.70
	W	14	1.58-1.80	1.70±0.02	0.07±0.01	3.86±0.73

TABLE 12  
MEASUREMENTS (IN MM.) OF *Absarokius noctivagus*

		N	O.R.	M
P <sup>1</sup>	L	2	2.30-2.50	2.40
	W	2	3.05-3.40	3.23
M <sup>1</sup>	L	2	2.15-2.20	2.18
	W	2	3.20-3.38	3.29
M <sup>2</sup>	L	2	2.05-2.20	2.13
	W	2	3.90-3.90	3.90
M <sup>3</sup>	L	1	1.50	1.50
	W	1	2.60	2.60
P <sub>4</sub>	L	3	2.38-3.00	2.63
	W	3	2.48-2.60	2.53
M <sub>1</sub>	L	4	2.20-2.40	2.32
	W	4	1.80-2.40	2.09
M <sub>2</sub>	L	6	2.10-2.40	2.26
	W	6	2.00-2.20	2.10
M <sub>3</sub>	L	5	2.20-2.70	2.41
	W	4	1.63-1.85	1.75

TABLE 13  
MEASUREMENTS (IN MM.) OF *Phenacolemur*

		<i>P. citatus</i>		<i>P. jepseni</i>		
	N	O.R.	M	N	O.R.	M
M <sup>3</sup>	L	1	2.00	2.00	—	—
	W	1	2.20	2.20	—	—
P <sub>4</sub>	L	1	3.35	3.35	—	—
	W	1	2.00	2.00	—	—
M <sub>1</sub>	L	3	2.75-2.90	2.85	1	2.30
	W	3	2.32-2.35	2.34	1	1.60
M <sub>2</sub>	L	3	2.80-3.00	2.92	—	—
	W	3	2.25-2.40	2.35	—	—

TABLE 14  
MEASUREMENTS (IN MM.) OF *Microsyops scottianus*

	N	O.R.	M
P <sup>1</sup> L	5	3.42-4.18	3.76
ant. W	5	4.05-4.90	4.65
M <sup>1</sup> L	10	3.10-4.30	3.83
ant. W	9	4.35-5.30	4.65
M <sup>2</sup> L	10	3.70-4.40	4.12
ant. W	9	4.68-5.55	5.05
M <sup>3</sup> L	5	3.60-4.25	4.00
ant. W	5	4.60-5.25	4.82



TABLE 15  
MEASUREMENTS (IN MM.) OF *Paramys copei*

	N	O.R.	M	s	V
P <sup>3</sup> L	2	1.52-1.90	1.71	—	—
W	2	1.90-2.40	2.15	—	—
P <sup>4</sup> L	8	2.85-3.40	3.14	—	—
W	8	3.50-4.30	3.86	—	—
M <sup>1</sup> L	8	3.30-3.60	3.45	—	—
W	8	3.32-4.05	3.72	—	—
M <sup>2</sup> L	11	3.30-3.90	3.57	—	—
W	11	3.62-4.35	3.91	—	—
M <sup>3</sup> L	4	3.38-4.00	3.67	—	—
W	5	2.97-3.60	3.53	—	—
I <sub>1</sub> L	26	3.30-4.70	3.92	—	—
W	29	2.13-3.90	2.47	—	—
P <sub>4</sub> L	19	3.16-3.85	3.53±0.04	0.16±0.03	4.56±0.74
W tal	19	2.55-3.63	3.13±0.06	0.26±0.04	8.40±1.36
W tri	18	2.39-3.40	2.78±0.06	0.24±0.04	8.74±1.46
M <sub>1</sub> L	35	3.03-3.90	3.48±0.03	0.20±0.02	5.80±0.69
W tal	31	2.80-3.70	3.28±0.04	0.23±0.03	7.07±0.89
W tri	31	2.75-3.62	3.10±0.04	0.25±0.03	7.97±1.01
M <sub>2</sub> L	42	3.25-4.04	3.64±0.03	0.23±0.02	6.21±0.68
W tal	41	3.18-4.13	3.60±0.04	0.25±0.03	6.97±0.77
W tri	42	3.15-4.10	3.55±0.03	0.23±0.02	6.42±0.70
M <sub>3</sub> L	26	3.70-4.75	4.19±0.06	0.30±0.04	7.11±0.99
W tal	24	3.00-3.68	3.31±0.04	0.21±0.03	6.40±0.92
W tri	24	2.80-3.90	3.40±0.05	0.25±0.04	7.26±1.05

TABLE 16  
MEASUREMENTS (IN MM.) OF *Paramys excavatus*

	N	O.R.	M
I <sup>1</sup> L	1	4.15	4.15
W	1	2.00	2.00
P <sup>4</sup> L	5	2.22-2.73	2.45
W	5	3.00-3.25	3.12
M <sup>1</sup> L	5	2.22-2.48	2.36
W	5	2.70-3.10	2.90
M <sup>2</sup> L	2	2.40-2.85	2.63
W	1	3.45	3.45
M <sup>3</sup> L	2	2.74-2.88	2.81
W	1	2.78	2.78
I <sub>1</sub> L	4	3.00-4.15	3.55
W	4	1.70-2.20	1.91
P <sub>4</sub> L	1	2.30	2.30
W tal	1	1.85	1.85
W tri	1	1.50	1.50

(TABLE 16, *continued*)

	N	O.R.	M
M <sub>1</sub> L	3	2.64-2.98	2.78
W tal	3	2.60-2.95	2.75
W tri	3	2.40-2.55	2.45
M <sub>2</sub> L	7	2.60-3.15	2.91
W tal	8	2.60-3.15	2.93
W tri	7	2.50-3.02	2.75
M <sub>3</sub> L	5	2.95-3.50	3.23
W tal	5	2.40-2.75	2.61
W tri	5	2.55-2.80	2.71

TABLE 17  
MEASUREMENTS (IN MM.) OF *Paramys francesi*

	N	O.R.	M	s	V
P <sup>3</sup> L	1	1.00	1.00	—	—
W	1	1.10	1.10	—	—
P <sup>4</sup> L	2	2.30-2.35	2.33	—	—
W	2	2.85-2.90	2.88	—	—
M <sup>1</sup> L	2	2.20-2.32	2.26	—	—
W	2	2.65-2.70	2.68	—	—
M <sup>2</sup> L	3	2.30-2.38	2.34	—	—
W	3	2.55-3.00	2.72	—	—
M <sup>3</sup> L	—	—	—	—	—
W	1	2.30	2.30	—	—
I <sub>1</sub> L	22	2.50-3.10	2.82±0.04	0.17±0.03	6.03±0.91
W	22	1.65-2.10	1.82±0.03	0.12±0.02	6.56±0.99
P <sub>4</sub> L	12	1.95-2.53	2.21±0.04	0.15±0.03	7.02±1.43
W tal	12	1.90-2.30	2.09±0.03	0.10±0.02	5.01±1.02
W tri	11	1.50-1.84	1.63±0.04	0.12±0.03	7.28±1.55
M <sub>1</sub> L	21	2.20-2.40	2.32±0.01	0.06±0.01	2.73±0.42
W tal	21	2.05-2.40	2.24±0.02	0.11±0.02	5.06±0.78
W tri	19	1.80-2.12	1.98±0.02	0.09±0.01	4.63±0.75
M <sub>2</sub> L	21	2.30-2.50	2.41±0.01	0.07±0.01	2.82±0.43
W tal	17	2.25-2.68	2.48±0.03	0.14±0.02	5.78±0.99
W tri	17	2.20-2.53	2.34±0.02	0.09±0.02	3.89±0.67
M <sub>3</sub> L	8	2.45-2.80	2.62	—	—
W tal	7	2.08-2.38	2.22	—	—
W tri	7	2.30-2.47	2.37	—	—

TABLE 18  
MEASUREMENTS (IN MM.) OF *Thisbenys perditus*

		N	O.R.	M
P <sup>4</sup>	L	2	2.60-3.00	2.80
	W	3	3.26-4.08	3.74
M <sup>1</sup>	L	1	2.65	2.65
	W	1	3.27	3.27
M <sup>2</sup>	L	2	3.48-3.51	3.50
	W	2	4.12-4.12	4.12
M <sup>3</sup>	L	3	3.15-4.00	3.58
	W	3	3.12-3.80	3.53
I <sub>1</sub>	L	5	3.20-3.50	3.32
	W	5	1.63-2.40	1.94
P <sub>4</sub>	L	7	2.87-3.70	3.06
	W tal	7	2.56-3.08	2.75
	W tri	7	2.55-3.02	2.82
M <sub>1</sub>	L	2	3.30-3.50	3.40
	W tal	2	3.12-3.30	3.21
	W tri	1	2.96	2.96
M <sub>2</sub>	L	6	3.60-4.00	3.72
	W tal	6	3.40-3.85	3.59
	W tri	6	3.43-3.65	3.56
M <sub>3</sub>	L	3	4.05-4.35	4.20
	W tal	3	3.28-3.70	3.52
	W tri	3	3.42-3.60	3.51

TABLE 19  
MEASUREMENTS (IN MM.) OF *Lophiparamys*

		<i>L. debequensis</i>			<i>L. woodi</i>		
		N	O.R.	M	N	O.R.	M
M <sup>1</sup>	L	—	—	—	2	2.30-2.30	2.30
	W	—	—	—	2	2.90-3.08	2.99
M <sup>2</sup>	L	—	—	—	2	2.30-2.38	2.34
	W	—	—	—	2	3.00-3.00	3.00
I <sub>1</sub>	L	3	1.80-2.02	1.88	—	—	—
	W	3	0.93-1.00	0.98	—	—	—
P <sub>4</sub>	L	1	1.55	1.55	—	—	—
	W tal	1	1.30	1.30	—	—	—
	W tri	1	1.00	1.00	—	—	—
M <sub>3</sub>	L	2	1.70-1.80	1.75	2	2.60-3.00	2.80
	W tal	2	1.40-1.45	1.43	2	2.20-2.60	2.40
	W tri	2	1.50-1.60	1.55	2	2.10-2.60	2.35



TABLE 20  
MEASUREMENTS (IN MM.) OF *Knightomys depressus*

		N	O.R.	M	s	V
I <sup>1</sup>	L	3	2.25-2.62	2.44	—	—
	W	3	1.02-1.23	1.13	—	—
M <sup>2</sup>	L	1	2.06	2.06	—	—
	W	1	2.28	2.28	—	—
I <sub>1</sub>	L	14	2.10-2.48	2.26±0.03	0.11±0.02	4.96±0.94
	W	16	1.10-1.70	1.27±0.04	0.16±0.03	12.32±2.18
P <sub>4</sub>	L	3	1.70-1.80	1.77	—	—
	W tal	3	1.45-1.58	1.53	—	—
	W tri	3	1.15-1.40	1.28	—	—
M <sub>1</sub>	L	14	1.70-1.93	1.85±0.02	0.07±0.02	3.71±0.70
	W tal	14	1.68-2.00	1.80±0.03	0.09±0.03	5.27±1.00
	W tri	13	1.50-1.65	1.57±0.01	0.05±0.01	2.99±0.59
M <sub>2</sub>	L	15	1.75-2.00	1.90±0.02	0.07±0.02	3.68±0.67
	W tal	14	1.78-2.00	1.90±0.02	0.07±0.02	3.45±0.65
	W tri	12	1.70-1.85	1.78±0.02	0.05±0.02	3.03±0.62
M <sub>3</sub>	L	11	2.05-2.22	2.09±0.03	0.11±0.03	5.30±1.13
	W tal	10	1.60-1.85	1.71±0.03	0.08±0.03	4.60±1.03
	W tri	10	1.65-1.90	1.75±0.02	0.07±0.02	4.27±0.95

TABLE 21  
MEASUREMENTS (IN MM.) OF *Didymictis*

		Lysite. <i>D. protenus</i>			Lost Cabin. <i>D. altidens</i>		
		N	O.R.	M	N	O.R.	M
P <sub>2</sub>	L	1	8.70	—	—	—	—
	W	1	2.95	—	—	—	—
P <sub>3</sub>	L	2	11.05-11.60	11.32	2	12.00-12.62	12.31
	W	2	4.38- 5.05	4.71	2	5.50- 5.67	5.58
P <sub>4</sub>	L	4	10.70-13.45	12.46	3	14.30-15.10	14.65
	W	5	5.00- 5.70	5.41	3	6.45- 6.70	6.65
M <sub>1</sub>	L	5	10.80-13.70	12.22	8	14.70-15.88	15.15
	W	6	7.20- 8.30	7.62	7	8.80- 9.72	9.18
M <sub>2</sub>	L	9	7.85- 9.50	8.30	11	8.28- 9.75	9.02
	W	9	4.85- 5.78	5.11	11	5.18- 6.45	5.81

TABLE 22  
MEASUREMENTS (IN MM.) OF *Viverravus*

		<i>V. lutosus</i>			<i>V. gracilis</i>		
		N	O.R.	M	N	O.R.	M
P <sub>4</sub>	L	3	4.65-5.00	4.80	8	5.15-5.70	5.37
	W	4	1.68-2.20	1.86	8	1.95-2.20	2.09
M <sub>1</sub>	L	3	4.40-5.20	4.73	10	5.32-6.40	5.74
	W	4	2.55-3.00	2.73	10	3.12-3.60	3.29
M <sub>2</sub>	L	1	3.70	3.70	3	4.00-4.33	4.21
	W	1	2.30	2.30	3	2.35-2.52	2.45

TABLE 23  
MEASUREMENTS (IN MM.) OF *Miacis*

		<i>M. exiguus</i>			<i>M. latidens</i>		
		N	O.R.	M	N	O.R.	M
P <sub>4</sub>	L	—	—	—	1	6.70	6.70
	W	—	—	—	1	2.75	2.75
M <sub>1</sub>	L	1	5.50	5.50	1	7.10	7.10
	W	—	—	—	1	4.80	4.80
M <sub>2</sub>	L	3	3.55-3.88	3.68	2	4.80-4.90	4.85
	W	3	2.60-2.85	2.72	2	3.70-4.00	3.85
M <sub>3</sub>	L	1	2.75	2.75	1	3.12	3.12
	W	1	2.30	2.30	1	2.50	2.50

TABLE 24  
MEASUREMENTS (IN MM.) OF *Vulpavus*

		<i>V. canavus</i>			<i>V. australis</i>		
		N	O.R.	M	N	O.R.	M
M <sup>1</sup>	L	2	5.90-6.80	6.35	—	—	—
	W	2	6.80-7.20	7.00	—	—	—
M <sup>2</sup>	L	1	5.20	5.20	—	—	—
	W	1	7.30	7.30	—	—	—
M <sup>3</sup>	L	1	6.85	6.85	—	—	—
	W	1	4.05	4.05	—	—	—
P <sub>4</sub>	L	7	5.60-6.45	6.10	—	—	—
	W	7	2.70-3.60	3.09	—	—	—
M <sub>1</sub>	L	13	8.20-7.10	7.67	2	6.70-6.90	6.80
	W	14	4.65-5.50	5.03	2	4.50-4.60	4.55
M <sub>2</sub>	L	10	4.90-5.82	5.51	2	4.70-4.80	4.75
	W	10	3.95-5.00	4.47	2	3.90-4.00	3.95
M <sub>3</sub>	L	2	4.80-4.85	4.83	1	3.78	3.78
	W	2	4.05-4.13	4.09	1	3.08	3.08

TABLE 25  
MEASUREMENTS (IN MM.) OF *Uintacyon asodes*

		N	O.R.	M
P <sup>3</sup>	L	1	6.00	6.00
	W	1	4.90	4.90
P <sup>4</sup>	L	1	9.10	9.10
	W	1	6.90	6.90
M <sup>1</sup>	L	2	6.25- 6.70	6.48
	W	2	10.30-11.50	10.90
P <sub>4</sub>	L	—	—	—
	W	1	3.60	3.60
M <sub>1</sub>	L	1	8.25	8.25
	W	1	5.25	5.25
M <sub>2</sub>	L	3	5.60- 6.00	5.80
	W	3	4.45- 4.64	4.53

TABLE 26  
MEASUREMENTS (IN MM.) OF *Esthonyx acutidens*

		N	O.R.	M
P <sup>2</sup>	L	2	5.50- 5.80	5.65
	W	2	3.60	3.60
P <sup>3</sup>	L	3	8.50- 9.80	9.27
	W	3	7.90- 9.50	8.73
P <sup>4</sup>	L	3	8.80- 9.40	9.07
	W	3	11.30-13.70	12.13
M <sup>1</sup>	L	4	8.60-10.00	9.18
	W	4	12.50-14.00	13.50
M <sup>2</sup>	L	4	9.20-11.00	9.88
	W	4	12.90-17.00	15.10
M <sup>3</sup>	L	2	8.10- 8.50	8.30
	W	2	15.40-16.20	15.80
M <sub>1</sub>	L	4	7.90- 8.70	8.29
	W	4	5.90- 7.25	6.46
M <sub>2</sub>	L	6	9.25- 9.50	9.29
	W	6	6.60- 7.40	7.10
M <sub>3</sub>	L	3	10.80-13.00	12.03
	W	3	5.90- 6.30	6.16

TABLE 27  
MEASUREMENTS (IN MM.) OF *Hyopsodus wortmani*

		N	O.R.	M	s	V
P <sup>3</sup>	L	1	2.30	2.30	—	—
	W	1	2.95	2.95	—	—
P <sup>4</sup>	L	3	2.40-2.60	2.47	—	—
	W	3	3.40-3.50	3.43	—	—
M <sup>1</sup>	L	5	2.92-3.22	3.14	—	—
	W	5	3.95-4.15	4.03	—	—
M <sup>2</sup>	L	5	3.30-3.48	3.36	—	—
	W	5	4.40-4.75	4.58	—	—
M <sup>3</sup>	L	5	2.32-2.75	2.55	—	—
	W	6	3.40-4.30	3.70	—	—
P <sub>4</sub>	L	12	2.60-3.20	2.85±0.06	0.21±0.04	7.37±1.50
	W	12	1.90-2.40	2.10±0.05	0.16±0.03	7.62±1.56
M <sub>1</sub>	L	17	2.95-3.60	3.29±0.05	0.21±0.04	6.38±1.09
	W	17	2.40-2.97	2.67±0.04	0.18±0.03	6.74±1.16
M <sub>2</sub>	L	27	3.00-3.90	3.48±0.04	0.20±0.03	5.75±0.78
	W	27	2.62-3.40	2.97±0.04	0.20±0.03	6.73±0.91
M <sub>3</sub>	L	16	3.40-4.40	3.88±0.06	0.27±0.05	6.96±1.23
	W	17	2.30-3.10	2.63±0.05	0.21±0.04	7.98±1.37



TABLE 28  
MEASUREMENTS (IN MM.) OF *Hyopsodus miticulus*

		N	O.R.	M	s	V
P <sup>3</sup>	L	1	3.10	3.10	—	—
	W	1	3.25	3.25	—	—
P <sup>4</sup>	L	3	2.85-3.20	3.07	—	—
	W	3	4.20-4.30	4.23	—	—
M <sup>1</sup>	L	5	3.30-4.00	3.75	—	—
	W	5	4.32-5.20	4.92	—	—
M <sup>2</sup>	L	2	3.62-4.25	3.94	—	—
	W	2	4.90-6.10	5.50	—	—
M <sup>3</sup>	L	3	3.35-3.75	3.60	—	—
	W	3	4.50-5.15	4.78	—	—
P <sub>3</sub>	L	2	2.80-3.22	3.01	—	—
	W	2	2.00-2.22	2.11	—	—
P <sub>4</sub>	L	16	3.20-3.80	3.43±0.04	0.17±0.03	5.06±0.89
	W	16	2.25-2.90	2.62±0.04	0.17±0.03	6.62±1.17
M <sub>1</sub>	L	49	3.52-4.45	4.03±0.03	0.20±0.02	4.96±0.50
	W	48	2.80-3.65	3.25±0.03	0.17±0.02	5.33±0.54
M <sub>2</sub>	L	61	3.90-4.95	4.30±0.03	0.22±0.02	5.20±0.47
	W	60	3.15-4.06	3.64±0.02	0.17±0.02	4.76±0.43
M <sub>3</sub>	L	35	4.30-6.50	5.00±0.08	0.47±0.06	9.38±1.12
	W	34	2.58-4.32	3.37±0.06	0.35±0.04	10.27±1.25

TABLE 29  
MEASUREMENTS (IN MM.) OF *Hyopsodus walcottianus*

		N	O.R.	M
P <sub>4</sub>	L	3	4.80-5.28	5.03
	W	2	3.35-3.60	3.48
M <sub>1</sub>	L	3	5.50-5.95	5.63
	W	2	4.16-4.55	4.36
M <sub>2</sub>	L	4	5.65-6.32	5.99
	W	3	4.85-5.30	5.01
M <sub>3</sub>	L	5	5.80-7.30	6.63
	W	4	4.00-4.82	4.31

TABLE 30  
MEASUREMENTS (IN MM.) OF *Phenacodus primaevus*

		N	O.R.	M
P <sup>4</sup>	L	1	9.10	9.10
	W	1	10.30	10.30
M <sup>1</sup>	L	3	9.90-10.70	10.26
	W	3	11.60-12.70	12.02
M <sup>2</sup>	L	12	9.20-10.80	10.04
	W	12	10.90-13.20	12.28
M <sup>3</sup>	L	6	7.75- 9.60	8.56
	W	6	8.87-11.21	10.51
P <sub>4</sub>	L	4	9.51-10.85	10.15
	W	4	7.00- 8.07	7.61
M <sub>1</sub>	L	3	10.90-11.73	11.21
	W	3	9.10-10.18	9.44
M <sub>2</sub>	L	6	10.05-11.70	11.05
	W	6	9.50-10.70	10.24
M <sub>3</sub>	L	7	10.48-11.73	11.05
	W	8	8.40- 9.00	8.78

TABLE 31  
MEASUREMENTS (IN MM.) OF *Phenacodus vortmani*

		N	O.R.	M	s	V
P <sup>4</sup>	L	1	8.20	8.20	—	—
	W	1	9.40	9.40	—	—
M <sup>1</sup>	L	1	8.30	8.30	—	—
	W	1	11.00	11.00	—	—
M <sup>2</sup>	L	1	7.80	7.80	—	—
	W	1	11.70	11.70	—	—
M <sup>3</sup>	L	3	6.25- 6.95	6.72	—	—
	W	3	8.60- 9.30	8.88	—	—
P <sub>4</sub>	L	6	7.50- 9.60	8.26±0.31	0.75±0.22	9.07±2.62
	W	6	5.25- 6.80	5.68±0.24	0.58±0.17	10.27±2.97
M <sub>1</sub>	L	10	7.45- 8.50	7.97±0.11	0.36±0.08	4.52±1.01
	W	9	6.40- 7.25	6.77±0.11	0.33±0.08	4.90±1.56
M <sub>2</sub>	L	9	7.70- 9.10	8.23±0.19	0.57±0.13	6.88±1.62
	W	9	6.70- 7.35	6.97±0.11	0.32±0.07	4.54±1.44
M <sub>3</sub>	L	8	7.70-10.10	8.64±0.27	0.76±0.19	8.82±2.20
	W	7	5.30- 6.90	6.02±0.20	0.54±0.14	8.94±2.39

TABLE 32  
MEASUREMENTS (IN MM.) OF *Hyracotherium vasaccense*

		N	O.R.	M	s	V
P <sup>3</sup>	L	5	6.83- 7.60	7.27	—	—
	W	5	6.60- 8.20	7.58	—	—
P <sup>4</sup>	L	17	6.20- 7.40	6.87±0.08	0.32±0.05	4.60±0.79
	W	17	7.40- 9.22	8.32±0.10	0.41±0.07	4.95±0.85
M <sup>1</sup>	L	37	7.30- 9.75	8.12±0.08	0.50±0.06	6.16±0.72
	W	35	8.08-11.15	9.54±0.13	0.77±0.09	8.05±0.96
M <sup>2</sup>	L	35	7.90- 9.90	8.76±0.10	0.57±0.07	6.56±0.78
	W	35	9.40-12.10	10.82±0.12	0.70±0.08	6.47±0.77
M <sup>3</sup>	L	32	6.88- 8.68	7.89±0.08	0.42±0.05	5.37±0.67
	W	32	8.75-10.90	9.56±0.08	0.42±0.05	4.44±0.55
P <sub>2</sub>	L	2	6.23- 6.35	6.29	—	—
	W	2	3.05- 3.22	3.14	—	—
P <sub>3</sub>	L	4	6.40- 6.85	6.80	—	—
	W	4	4.10- 4.60	4.40	—	—
P <sub>4</sub>	L	27	6.50- 8.00	7.07±0.08	0.42±0.06	6.00±0.82
	W	27	4.30- 5.58	5.01±0.07	0.35±0.05	6.91±0.94
M <sub>1</sub>	L	30	6.75- 8.20	7.72±0.08	0.42±0.05	5.50±0.71
	W	30	4.85- 6.10	5.54±0.05	0.28±0.04	5.10±0.66
M <sub>2</sub>	L	41	7.00- 9.20	8.25±0.05	0.35±0.04	4.20±0.46
	W	41	5.00- 6.45	5.89±0.05	0.33±0.04	5.63±0.62
M <sub>3</sub>	L	36	9.70-12.80	10.98±0.10	0.62±0.07	5.69±0.67
	W	37	4.80- 6.75	5.54±0.06	0.36±0.04	6.51±0.76

TABLE 33  
MEASUREMENTS (IN MM.) OF *Hyracotherium*

		<i>H. craspedotum</i>			<i>H. index</i>		
		N	O.R.	M	N	O.R.	M
P <sup>4</sup>	L	2	7.75- 8.00	7.88	1	6.10	6.10
	W	2	9.43- 9.70	9.57	1	7.00	7.00
M <sup>1</sup>	L	2	8.60- 8.60	8.60	1	6.53	6.53
	W	2	10.90-11.00	10.95	1	7.22	7.22
M <sup>2</sup>	L	3	9.80-10.90	10.18	1	6.70	6.70
	W	3	12.20-13.52	12.66	1	8.00	8.00
M <sup>3</sup>	L	7	8.92-10.00	9.47	—	—	—
	W	7	10.70-12.20	11.43	—	—	—
P <sub>3</sub>	L	2	7.00- 7.50	7.25	—	—	—
	W	2	4.75- 5.50	5.13	—	—	—
P <sub>4</sub>	L	5	7.78- 8.30	8.06	—	—	—
	W	5	5.70- 6.40	6.03	—	—	—
M <sub>1</sub>	L	9	8.60- 9.30	8.98	1	5.80	5.80
	W	9	6.15- 7.08	6.65	1	3.90	3.90
M <sub>2</sub>	L	16	9.20-10.90	10.10	1	8.22	8.22
	W	16	6.55- 8.40	7.70	1	4.30	4.30
M <sub>3</sub>	L	4	12.50-14.10	13.45	1	8.22	8.22
	W	4	6.70- 7.80	7.23	1	4.30	4.30



TABLE 34  
MEASUREMENTS (IN MM.) OF *Lambdotherium popoagicum*

		N	O.R.	M	s	V
P <sub>2</sub>	L	11	6.80- 8.15	7.61±0.14	0.47±0.10	6.16±1.31
	W	12	3.85- 4.80	4.29±0.07	0.25±0.05	5.71±1.17
P <sub>3</sub>	L	15	7.90- 9.65	8.95±0.11	0.44±0.08	4.87±0.89
	W	15	5.10- 6.65	5.83±0.10	0.40±0.70	6.86±1.25
P <sub>4</sub>	L	34	8.50-10.00	9.24±0.07	0.41±0.05	4.46±0.54
	W	34	6.40- 8.00	7.05±0.06	0.33±0.04	4.70±0.57
M <sub>1</sub>	L	37	9.95-12.20	11.24±0.09	0.57±0.07	5.11±0.59
	W	37	7.32- 8.85	8.16±0.06	0.35±0.04	4.24±0.49
M <sub>2</sub>	L	37	10.85-13.30	12.38±0.09	0.53±0.06	4.27±0.50
	W	37	8.20-10.00	8.10±0.07	0.40±0.05	4.44±0.52
M <sub>3</sub>	L	32	15.00-17.90	16.74±0.13	0.74±0.09	4.43±0.55
	W	33	8.05-11.40	8.90±0.10	0.57±0.07	6.46±0.79

TABLE 35  
MEASUREMENTS (IN MM.) OF *Eotitanops borealis*

		N	O.R.	M
P <sub>4</sub>	L	5	11.00-12.90	12.49
	W	5	6.80- 8.40	7.91
M <sub>1</sub>	L	6	14.83-18.10	16.77
	W	5	9.53-11.80	10.75
M <sub>2</sub>	L	5	17.40-20.40	19.52
	W	5	10.31-13.40	12.18
M <sub>3</sub>	L	7	23.30-29.45	25.41
	W	8	10.30-13.40	11.77

TABLE 36  
MEASUREMENTS (IN MM.) OF *Diacodexis metsiacus*

		N	O.R.	M
M <sup>2</sup>	L	1	4.30	4.30
	W	1	5.70	5.70
P <sub>3</sub>	L	1	5.30	5.30
	W	1	1.90	1.90
P <sub>4</sub>	L	7	4.35-5.20	4.68
	W	7	2.25-2.80	2.49
M <sub>1</sub>	L	5	3.60-3.90	3.75
	W	5	2.70-3.08	2.96
M <sub>2</sub>	L	8	3.80-4.30	4.03
	W	6	3.30-3.70	3.46
M <sub>3</sub>	L	9	4.40-5.10	4.88
	W	9	3.00-3.50	3.29

TABLE 37  
MEASUREMENTS (IN MM.) OF *Diacodexis secans*

		N	O.R.	M	s	V
P <sup>3</sup>	L	1	4.80	4.80	—	—
	W	1	3.10	3.10	—	—
P <sup>4</sup>	L	3	3.80-5.15	4.30	—	—
	W	3	4.90-5.90	5.33	—	—
M <sup>1</sup>	L	2	4.40-4.80	4.60	—	—
	W	2	5.40-5.65	5.52	—	—
M <sup>2</sup>	L	4	4.55-5.00	4.88	—	—
	W	4	6.55-7.00	6.74	—	—
M <sup>3</sup>	L	5	4.05-4.80	4.50	—	—
	W	5	5.80-6.80	6.40	—	—
P <sub>3</sub>	L	3	5.30-6.60	6.03	—	—
	W	3	1.90-2.20	2.08	—	—
P <sub>4</sub>	L	10	5.15-6.44	5.63±0.13	0.40±0.09	7.17±1.60
	W	10	2.73-3.33	2.99±0.07	0.22±0.05	7.23±1.62
M <sub>1</sub>	L	16	3.75-5.00	4.48±0.08	0.32±0.06	7.03±1.24
	W	16	3.20-4.02	3.65±0.06	0.24±0.04	6.68±1.18
M <sub>2</sub>	L	18	4.25-5.25	4.70±0.07	0.31±0.05	6.57±1.10
	W	18	3.75-4.90	4.38±0.08	0.33±0.05	7.43±1.24
M <sub>3</sub>	L	15	5.57-7.30	6.24±0.10	0.40±0.07	6.43±1.17
	W	16	3.33-4.85	4.23±0.09	0.34±0.06	8.05±1.42

TABLE 38  
MEASUREMENTS (IN MM.) OF *Antiacodon vanvaleni*

		N	O.R.	M
P <sub>4</sub>	L	1	5.25	5.25
	W	1	2.60	2.60
M <sub>1</sub>	L	3	4.30-4.55	4.47
	W	4	3.18-3.90	3.35
M <sub>2</sub>	L	5	4.60-5.00	4.84
	W	5	3.58-4.05	3.77
M <sub>3</sub>	L	3	5.22-6.05	5.59
	W	3	3.20-3.50	3.38

TABLE 39  
MEASUREMENTS (IN MM.) OF *Bunophorus etsagicus*

		N	O.R.	M	s	V
P <sup>4</sup>	L	1	5.90	5.90	—	—
	W	1	6.77	6.77	—	—
M <sup>1</sup>	L	3	6.48- 7.00	6.66	—	—
	W	3	7.80- 8.60	8.30	—	—
M <sup>2</sup>	L	4	7.10- 7.65	7.32	—	—
	W	4	9.30-10.45	9.80	—	—
M <sup>3</sup>	L	4	6.55- 7.68	7.13	—	—
	W	4	9.45- 9.50	9.49	—	—
P <sub>3</sub>	L	1	7.60	7.60	—	—
	W	1	3.00	3.00	—	—
P <sub>4</sub>	L	7	7.15- 7.90	7.50	—	—
	W	7	3.90- 5.00	4.33	—	—
M <sub>1</sub>	L	15	6.60- 7.40	7.09±0.06	0.24±0.04	3.45±0.63
	W	15	5.80- 6.95	6.41±0.10	0.37±0.07	5.84±1.07
M <sub>2</sub>	L	16	6.90- 8.20	7.60±0.08	0.30±0.05	3.95±0.70
	W	16	6.50- 7.40	6.99±0.07	0.28±0.05	4.05±0.72
M <sub>3</sub>	L	13	8.20-10.32	9.31±0.14	0.52±0.10	5.58±1.09
	W	13	6.50- 7.68	6.83±0.10	0.35±0.07	5.07±1.00

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AN ANNOTATED LIST OF THE VASCULAR FLORA  
OF BUTLER COUNTY, PENNSYLVANIA

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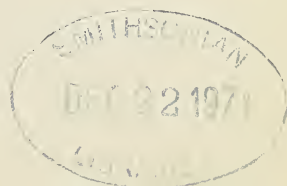
Butler County is situated in west-central Pennsylvania near the Ohio line. It contains 508,672 acres, of which 156,373 are forested. Of the 2810 acres publicly owned, 2720 are State Game Lands. Although this is not a leading farm county, there are 158,955 acres under cultivation. The principal creeks in the area are Muddy, Connoquenessing, Breakneck, and Slippery Rock, draining into the Beaver River, and Buffalo, Bear, and Scrubgrass, draining into the Allegheny River.

Butler County is situated on a high plateau, the Harrisburg peneplain, consisting of gently rolling hills and wide valleys that have been deeply trenched by the tributaries to the Ohio and Allegheny rivers. The surface of this peneplain now ranges from an elevation of 1500 feet above sea level in the northern part to some 1200 feet in the south. The county lies chiefly within the floristic area called the Hill Section, that comprises the southwestern part of Pennsylvania. Oak-hickory forests are characteristic of these uplands and hilltops. The northwest corner of the county, bordering on Mercer and Lawrence counties, lies within the glaciated area. Here the Wisconsin terminal moraine, 10,000 years old, consists of an irregular line of knolls, hills, and ridges of various mixtures of sand, gravel, and boulders. Here, also, are numerous kettle-shaped depressions, some of which contain ponds, swamps, and bogs.

Butler County is in an area that receives 38-42 inches of rainfall annually. The length of the growing season, figured from the last killing frost in spring to the first killing frost in autumn, varies from 140 days in the northern half of the County to 150 and 160 days toward the southern boundary. The 160 frost-free days occur only in the extreme southwest corner.

Publication of this List has been made possible by a gift from Mrs. Greta S. Heckett, to whom Carnegie Museum is most grateful.

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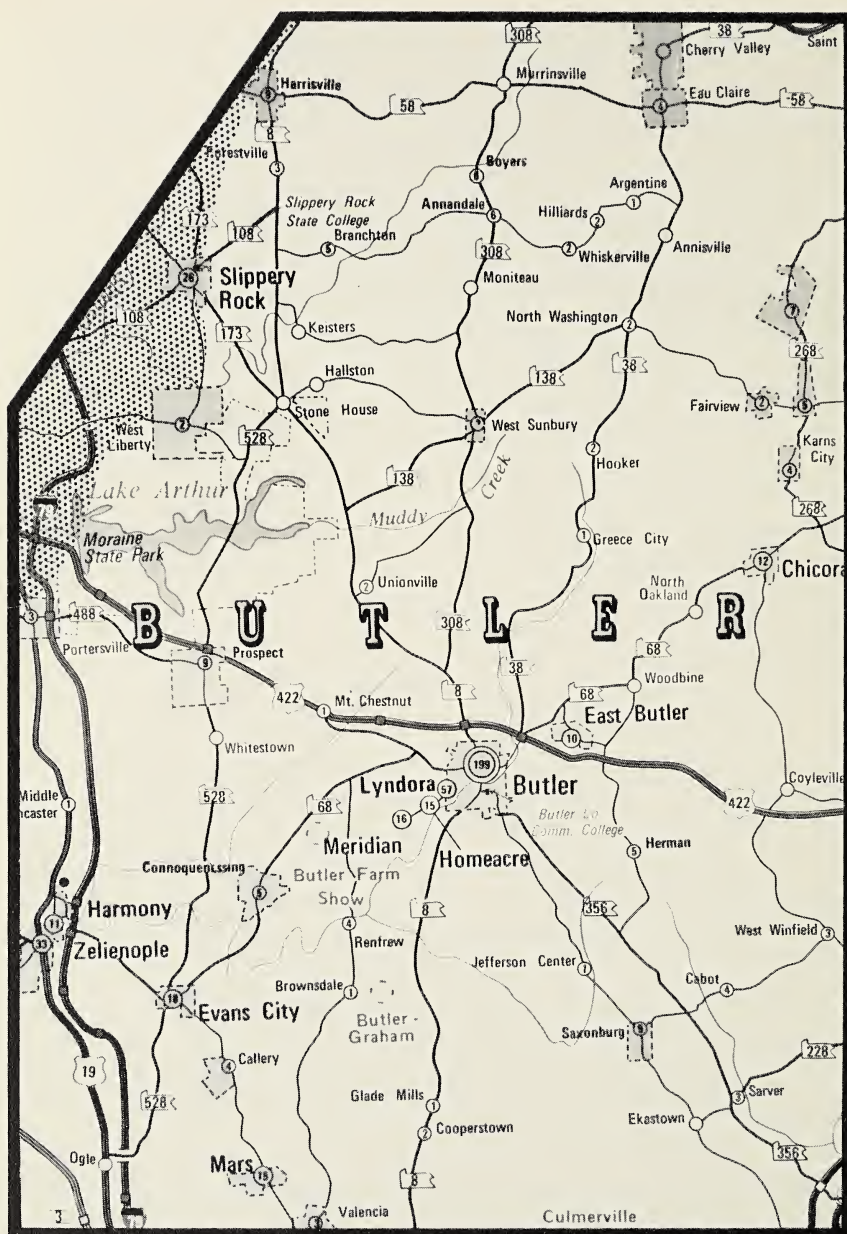


Fig. 1. Map of Butler County, Pennsylvania, with dotted area in northwest corner indicating approximate maximum advance of glacial ice.

The soils of the county are of the gray-brown podzolic type, of which three series occur here. The Raynes-Gilpin soil series is confined to the eastern edge, in a narrow band that widens along the northern border. In the glaciated area in the northwest section is the Wooster-Mahoning soil series. Most of the county is covered by the Westmoreland soil series, which extends up the slopes to the hilltops and uplands of the Harrisburg peneplain. The soils of this series, more fertile and better developed, were derived from the prevailing shales and sandstones of the upper Carboniferous, and are generally grayish brown and friable, but shallow.

Butler County lies in the Deciduous Forest vegetation zone. Its original upland forest was dominated by white oak, accompanied by mockernut and shagbark hickories, and by smaller numbers of black cherry, white ash, red maple, and some Juneberry, summer grape, maple-leaved viburnum, and poison ivy. This type of forest is called White Oak-Hickory forest association and is found on the upper slopes and hilltops. On the well-drained fertile soils of valley and ravine slopes occurs the Red Oak-Basswood-White Ash forest association, accompanied by beech, sugar maple, red maple, black cherry, and tulip tree. Hemlock still occurs on steep-sided ravines, especially in the northwest corner. Along meandering Muddy Creek there are swamp forests of American elm, red maple, and black ash.

The blazing-star, a prairie plant, spreads over an area of several acres near the Old Stone House (restored historic site) in northwestern Butler County. A few miles to the east are several other patches of this prairie plant, all occurring along what was the shore of a silt-laden, glacial lake (Lake Arthur now covers part of that site). One of these patches contains a dense stand of big bluestem grass, once abundant on the original Midwestern prairie.

A shrub-sedge bog, west of West Liberty, is the southernmost bog in western Pennsylvania. It is rapidly filling up with shrubs, and no longer has any open water. In Mercer County, a larger bog containing tamarack lies southwest of Grove City near the border of Butler County. This is rapidly becoming a swamp forest.

Other habitats are cattail marshes, wet meadows, dry meadows, and old fields.

In this article, the sequence of families and the nomenclature, with minor exceptions, follows that of Gray's Manual of Botany (ed. 8, 1950). The genera and species are listed alphabetically under the families. If a

species is considered common in the county, only the scientific and the common names are given. If it is infrequent or occasional throughout the county, an asterisk precedes the name. If the species is rare, the locality of collection, the date, and the collector's name have been added. Names of introduced or adventive plants are in small capitals. Collectors names, following the collection data, are abbreviated as follows:

LKH: LeRoy K. Henry, Curator of Plants, Carnegie Museum.

OEJ: Otto E. Jennings, late Director of Carnegie Museum, formerly Curator of Botany.

FHB: Fred H. Beer, Botanical Society of Western Pennsylvania member, who accompanied LKH on collecting trips .

CMB: Charles M. Boardman, Research Associate, Section of Plants, Carnegie Museum.

JB: John Bright, late member of the Botanical Society of Western Pennsylvania.

WEB: Werner E. Buker, Research Associate, Section of Plants, Carnegie Museum.

Collecting in Butler County for the Carnegie Museum Herbarium began in the early 1900's and has continued to the present. Most of the collectors have been members of the Botanical Society of Western Pennsylvania and the staff of the Section of Plants at Carnegie Museum.

The following annotated list contains 1094 species, varieties, forms, and hybrids, in 428 genera. Native species total 965, and introduced ones, 129. Those species considered rare in the county number 340. This last figure may not be accurate, since future collecting may very well add more localities for some of the species now included in this total.

Phylum Pteridophyta  
Family EQUISETACEAE  
*Equisetum*

*E. arvense* L.

Field Horsetail

*E. HYEMALE* var. *affine* (Engelm.) A.A. Eat.

Common Scouring Rush

Family LYCOPODIACEAE  
*Lycopodium*

*L. clavatum* L.

Running Clubmoss

*L. flabelliforme* (Fern.) Blanchard

Running-pine

*L. lucidulum* Michx.

Shining Clubmoss

*L. obscurum* L.

Flat-branch Ground-pine

*L. obscurum* var. *dendroideum* (Michx.) D.C. Eat.

Round-branch Ground-pine



- L. tristachyum* Pursh Ground-cedar  
 2 mi. N. of Stone House, on Rt. 8, W. of Keisters, 9/19/60, WEB.  
 Todd Sanctuary, 2 mi. S. of Leasuresville, 7/29/70, LKH.

## Family SELAGINELLACEAE

*Selaginella*

- S. apus* Spring Meadow Spike-moss

## Family OPHIOGLOSSACEAE

*Botrychium*

- B. dissectum* Spreng. Dissected Grape Fern  
*B. lanceolatum* var. *angustisegmentum* Pease and Moore Lanceolate Grape Fern  
 2 mi. N. of Unionville, along Rt. 8, 9/4/65, WEB.  
 Woods along dirt road, between Parkers Landing and Bruin, 7/14/70, LKH and WEB.  
*B. matricariifolium* A. Br. Matricary Grape Fern  
 Woods along dirt road, between Parkers Landing and Bruin, 7/14/70, LKH and WEB.  
*B. obliquum* Muhl. Coarse-lobed Grape Fern  
*B. oneidense* House Blunt-lobed Grape Fern  
 Little Buffalo Creek at Monroe Station, 9/19/62, LKH.  
 2 mi. S.W. of West Liberty, 9/29/54, LKH.  
*B. virginiana* (L.) Sw. Rattlesnake Fern

## Family OSMUNDACEAE

*Osmunda*

- O. cinnamomea* L. Cinnamon Fern  
*O. claytoniana* L. Interrupted Fern  
*O. regalis* var. *spectabilis* (Willd.) Gray Royal Fern

## Family SCHIZAEACEAE

*Lygodium*

- L. palmatum* (Bernh.) Swartz Climbing Fern  
 Lancaster Township, near Middle Lancaster village, 3 mi. N. of Zelienople,  
 7/30/67, Fred Lochner.

## Family POLYPODIACEAE

*Adiantum*

- A. pedatum* L. Maidenhair Fern

*Asplenium*

- A. montanum* Willd. Mountain Spleenwort  
 Plains Church, 8/31/09, OEJ.  
*A. pinnatifidum* Nutt. Pinnatifid Spleenwort  
 2 mi. S. of Leasuresville, 8/6/50, Carl and Dorothy Auerswald.  
*A. platyneuron* Oakes Ebony Spleenwort  
*A. trichomanes* L. Maidenhair Spleenwort  
 Glade Mills, 4/20/13, OEJ and A. R. Hillard.



*Athyrium*

- A. angustum* Presl Northeastern Lady Fern  
*A. angustum* var. *elatus* (Link) Butters Tall Upland Lady Fern  
*A. angustum* var. *rubellum* (Gilb.) Butters Reddish Upland Lady Fern  
*A. asplenoides* A. Eat. Southern Lady Fern  
*A. thelypteroides* (Michx.) Desv. Silvery Glade Fern

*Camptosorus*

- C. rhizophyllus* (L.) Link Walking Fern

*Cystopteris*

- C. bulbifera* (L.) Bernh. Bulblet Fern  
 Near Slippery Rock, 7/13/40, A. G. Shields.  
*C. fragilis* (L.) Bernh. Brittle Fern  
*C. fragilis* var. *mackayii* Lawson MacKay's Brittle Fern  
*C. protrusa* Weath. Lowland Brittle Fern  
 Along Wolf Creek, 1.25 mi. S.W. of Christleys Mills, 5/22/65, LKH.  
 0.8 mi. S.W. of Butler, along Bonnier Run, 5/23/61, LKH and FHB.

*Dennstaedtia*

- D. punctilobula* (Michx.) Moore Hay-scented Fern

*Dryopteris*

- D. x boottii* (Tuckerm.) Underw. Boott's Wood Fern  
 1 mi. E. of Boydstown, along tributary of Connoquenessing Creek, 8/21/34, W. R. Van Dersal.  
*D. cristata* (L.) Gray Crested Wood Fern  
*D. intermedia* (Muhl.) Gray Evergreen Wood Fern  
*D. marginalis* (L.) Gray Leathery Wood Fern  
*D. marginalis* f. *elegans* (J. Robins.) F. W. Gray  
 Woods, southeast edge of Hilliards, 8/10/54, LKH.  
*D. spinulosa* (O. F. Muell.) Walt. Toothed Wood Fern  
*D. x. triploidea* Wherry Triploid Wood Fern

*Matteuccia*

- M. pennsylvanica* Raymond Ostrich Fern  
 Slippery Rock Creek, from Rt. 488 to mouth of Wolf Creek, 4/24/58, LKH and FHB.

*Onoclea*

- O. sensibilis* L. Sensitive Fern

*Phegopteris*

- P. hexagonoptera* Fee Broad Beech Fern

*Polypodium*

- P. virginianum* L. Rock-cap Fern

*Polystichum*

- P. acrostichoides* (Michx.) Schott Christmas Fern  
*P. acrostichoides* f. *crispum* Clute Crested form of Christmas Fern  
 Todd Sanctuary, 2 mi. S. of Leasuresville, 7/29/70, LKH.  
*P. acrostichoides* f. *incisum* (Gray) Gilb. Incised form of Christmas Fern  
 Field at Middle Lancaster, 10/24/70, Fred Lochner.

*Pteridium*

- P. aquilinum* var. *latiusculum* (Desv.) Underw. Bracken

*Thelypteris*

- T. noveboracensis* (L.) Nieuwl. New York Fern  
*T. palustris* var. *pubescens* Fern. Marsh Fern

Phylum Spermatophyta  
 Subphylum Gymnospermae  
 Family TAXACEAE  
*Taxus*

- T. canadensis* Marsh. American Yew

Family PINACEAE  
*Juniperus*

- J. virginiana* L. Red Cedar  
 Woods at Butler Reservoir, 9 mi. N. of Butler, 5/19/55, LKH. Probably planted.  
 Plains Church, 8/31/09, OEJ. Probably planted.

*Larix*

- L. laricina* (DuRoi) K. Koch Larch  
 Muddy Creek area, E. of Portersville Station, 9/2/65, LKH.

*Pinus*

- P. banksiana* Lamb. Jack Pine  
 Planted on old spoil bank of strip-mine, along Findlay Run at Pipestem Road, 3 mi. N.W. of West Sunbury, oak-maple woods, 5/21/69, LKH.  
*P. rigida* Mill. Pitch Pine  
 Brush Creek Swamp, near Dutlih Church, 4/26/08, OEJ.  
 Along Little Buffalo Creek at Monroe Station, 1/22/1899, W. E. Clyde Todd.  
*P. strobus* L. White Pine  
 Along North Branch of Bear Creek, about 1 mi. N.E. of Bruin, 8/4/70, Fred Lochner.  
*P. virginiana* Mill. Scrub Pine  
 Woods at Butler Reservoir, 9 mi. N. of Butler, 5/19/55, LKH. Probably planted.

*Tsuga*

- T. canadensis* (L.) Carr. Hemlock



## Family HYDROCHARITACEAE

*Elodea*\**E. canadensis* Michx.

Waterweed

*E. nuttallii* (Planch.) St. John

Nuttall's Waterweed

Slippery Rock, 6/23/25, OEJ.

Wolf Creek, N. of Slippery Rock, 8/13/22, OEJ.

## Family GRAMINEAE

*Agropyron**A. repens* (L.) Beauv.

Witch Grass

*A. trachycaulum* var. *glaucum* (P. & M.) Malte

Bearded Wheat Grass

Ribold, 6/28/36, JB.

*Agrostis**A. alba* L.

Redtop

*A. perennans* (Walt.) Tuckerm.

Upland Bent

*A. perennans* var. *aestivalis* Vasey

Thin Grass

*Andropogon*\**A. gerardii* Vitman

Big Bluestem

*A. virginicus* L.

Broom Sedge

*Anthoxanthum**A. ODORATUM* L.

Sweet Vernal Grass

*Aristida*\**A. dichotoma* Michx.

Poverty Grass

*Brachyelytrum**B. erectum* var. *septentrionale* Babel.

Bearded Short-husk

3 mi. S.E. of Renfrew, 7/23/39, OEJ.

*Bromus**B. latiglumis* f. *incanus* (Shear) Fern.

Broad-glumed Brome Grass

Elliottsville, 8/19/22, OEJ.

*B. purgans* L.

Hairy Wood Chess

*B. SECALINUS* L.

Cheat or Chess

*Calamagrostis**C. canadensis* (Michx.) Nutt.

Bluejoint Grass

Along Rt. 8 and Slippery Rock Creek, S.E. of Slippery Rock, 7/23/44, OEJ.

*Cinna**C. arundinacea* L.

Wood Reed Grass

*Dactylis**D. GLOMERATA* L.

Orchard Grass



*Danthonia**D. spicata* (L.) Beauv.

Poverty Grass or White Oat Grass

*Digitaria*\**D. ISCHAEMUM* (Schreb.) Muhl.

Small Crab-grass

*D. SANGUINALIS* (L.) Scop.

Large Crab-grass or Finger Grass

*Echinochloa**E. CRUS-GALLI* (L.) Beauv.

Barnyard Grass

\**E. Pungens* (Poir.) Rydb.

Barnyard Grass

*Eleusine*\**E. INDICA* (L.) Gaertn.

Wiregrass

*Elymus**E. canadensis* L.

Wild Rye

*E. riparius* Wieg.

Riverbank Wild Rye

*E. virginicus* L.

Terrell Grass

*E. virginicus* var. *hirsutiglumis* (Schreb.) Hitchc.

Hairy Terrell Grass

*Eragrostis**E. hypnoides* (Lam.) BSP.

Creeping Love Grass

\**E. pectinacea* (Michx.) Nees

Love Grass

*Festuca**F. ELATIOR* L.

Meadow Fescue

*Glyceria**G. canadensis* (Michx.) Trin.

Rattlesnake Grass

*G. laxa* Schribn.

Loose Rattlesnake Grass

3 mi. E. of Portersville Station, 9/2/65, LKH.

*G. pallida* (Torr.) Trin.

Pale Manna Grass

Slippery Rock, 6/21/24, OEJ.

\**G. septentrionalis* Hitchc.

Floating Manna Grass

*G. striata* (Lam.) Hitchc.

Striate Manna Grass

*Holcus**H. LANATUS* L.

Velvet Grass

*Hystrix**H. patula* Moench.

Bottle-brush Grass

*Leersia**L. oryzoides* (L.) Sw.

Rice Cut-grass

*L. virginica* Willd.

Virginia Cut-grass

*Milium**M. effusum* L.

Millet Grass

Slippery Rock, 6/23/28, OEJ.

*Muhlenbergia*

- M. frondosa* (Poir.) Fern. Satin Grass  
*M. mexicana* (L.) Trin. Mexican Dropseed  
 Bog, 1.5 mi. W. of West Liberty, 9/5/51, LKH and WEB.  
 \**M. schreiberi* J. F. Gmel. Dropseed  
 \**M. sylvatica* Torr. Wood Dropseed  
*M. tenuiflora* (Willd.) BSP. Slender Satin Grass  
 Near Renfrew, 9/4/26, JB.

*Panicum*

- P. boscii* Poir. Bosc's Panic Grass  
 Little Buffalo Creek, 5/30/46, WEB.  
 \**P. capillare* L. Old Witch Grass  
*P. clandestinum* L. Hidden Panic Grass  
*P. commutatum* var. *ashei* (Pearson) Fern. Ashe's Panic Grass  
 Hillside above mouth of Little Buffalo Creek, 5/30/46, WEB.  
 Near Renfrew, 6/19/20, E. M. Gress.  
 \**P. dichotomiflorum* Michx. Forking Panic Grass  
*P. gattingeri* Nash Gattinger's Panic Grass  
 4 mi. N.E. of Harmony, Sept. 1927, LKH.  
*P. lanuginosa* var. *implicatum* (Scribn.) Fern. Tangled Panic Grass  
*P. latifolium* L. Broad-leaved Panic Grass  
*P. linearifolium* Scribn. Linear-leaved Panic Grass  
 Slippery Rock, 6/23/25, OEJ.  
 Little Buffalo Creek, 5/30/41, WEB.  
 \**P. microcarpon* Muhl. Tiny-fruited Panic Grass  
*P. stipitatum* Nash Stem-fruited Panic Grass  
 Muddy Creek near Rt. 422, 12 mi. N.W. of Butler, 9/14/51, LKH and FHB.  
 Muddy Creek at Isle, 10/5/50, LKH and FHB.  
*P. virgatum* L. Switch Grass

*Phalaris*

- P. arundinacea* L. Reed Canary Grass

*Phleum*

- P. PRATENSE* L. Timothy

*Poa*

- P. alsodes* Gray Tufted Bluegrass  
*P. ANNUA* L. Annual Bluegrass  
*P. COMPRESSA* L. Canada Bluegrass  
*P. cuspidata* Nutt. Cusped Bluegrass  
*P. pratensis* L. Kentucky Bluegrass

*Schizachne*

- S. purpurascens* (Torr.) Swallen False Melic Grass  
 Near Butler Reservoir, 9 mi. N. of Butler, 5/20/45, OEJ.

*Setaria*

- S. GLAUCA* (L.) Beauv.  
*S. ITALICA* (L.) Beauv.  
 Ribold, 9/17/49, OEJ.

Yellow Foxtail  
 Foxtail Millet

*Sphenopholis*

- S. intermedia* Rydb.  
 Portersville Station, 6/24/59, LKH and WEB.  
 \**S. nitida* (Spreng.) Scribn.

Slender Wedge Grass  
 Shining Wedge Grass

## Family CYPERACEAE

*Bulbostylis*

- B. capillaris* (L.) C. B. Clarke  
 9 mi. S.E. of Slippery Rock, along Rt. 8, 7/23/44, OEJ.  
 Butler-Armstrong county border, along Buffalo Creek, 1-3 mi. N. of Freeport, 6/10/44, OEJ.

Hairlike Bulbostylis

*Carex*

- C. annectens* var. *xanthocarpa* (Bickn.) Wieg.  
 Tributary of Bear Run, 2 mi. N.W. of Fairview, 6/27/61, LKH and FHB.  
 Along Muddy Creek, 1 mi. W. of Isle, 7/6/60, LKH.  
*C. argyrantha* Tuck.  
 Just north of Bruin, on Rt. 268, 5/31/48, WEB.  
*C. artitecta* Mackenz.  
*C. bushii* Mackenz.  
 Jennings Blazing-star Prairie at Stone House, S. of Slippery Rock, at Rts. 8 and 78, 6/7/55, OEJ.  
*C. caroliniana* Schwein.  
 Floodplain of Muddy Creek at Isle, 6/14/50, LKH and FHB.  
*C. cephalophora* Muhl.  
*C. communis* Bailey  
*C. comosa* Boott  
 Slippery Rock, 6/23/25, OEJ.  
 \**C. convoluta* Mackenz.  
*C. crinita* Lam.  
*C. cristatella* Britt.  
 Near McBride, 7/11/28, JB.  
*C. emoryi* Dew.  
 Mouth of Thorn Creek at Renfrew, 6/13/26, JB.  
 About 2 mi. N. of Freeport, along Buffalo Creek, Armstrong-Butler county line, 6/10/44, OEJ.  
*C. flaccosperma* var. *glaucodea* (Tuckerm.) Kukenth.  
 Plains Church, Rt. 528 in Cranberry Twp., 6/15/29, OEJ.  
*C. gracilescens* Steud.  
*C. gracillima* Schwein.  
*C. granularis* Muhl.  
 Along south branch of Slippery Rock Creek, 2-3 mi. S.E. of Bovard, 6/9/55, LKH.  
*C. gynandra* Schwein.

Yellow-fruited Sedge

Silvery-flowered Sedge

Emmon's Sedge

Bush's Sedge

Carolina Sedge

Oval-headed Sedge

Fibrous-rooted Sedge

Bearded Sedge

Convolute Sedge

Fringed Sedge

Crested Sedge

Emory's Sedge

Glaucous Sedge

Slender Sedge

Graceful Sedge

Granular Sedge

Nodding Sedge

- C. hirsutella* Mackenz. Hirsute Sedge  
*\*C. hystericina* Muhl. Porcupine Sedge  
*C. intumescens* Rudge Inflated Sedge  
*C. laevivaginata* (Kukenth.) Mackenz. Smooth-sheathed Sedge  
 Renfrew, 6/13/26, JB.  
*C. laxiculmis* Schw. Spreading Sedge  
 Woods at Butler Reservoir, 9 mi. N. of Butler, 5/19/55, LKH.  
*C. laxiflora* Lam. Two-edged Sedge  
*C. leavenworthii* Dewey Leavenworth's Sedge  
 0.5 mi. S. of Criders Corners, 9/17/45, LKH.  
*C. lupulina* Muhl. Hop Sedge  
*C. lurida* Wahlenb. Sallow Sedge  
*C. normalis* Mackenz. Larger Straw Sedge  
*C. pennsylvanica* Lam. Pennsylvania Sedge  
*\*C. plantaginea* Lam. Plantain-leaved Sedge  
*\*C. platyphylla* Carey Wide-leaved Sedge  
*\*C. prasina* Wahlenb. Drooping Sedge  
*C. rosea* Schkuhr. Stellate Sedge  
*C. scoparia* Schkuhr. Pointed Broom Sedge  
*C. squarrosa* L. Squarrose Sedge  
 Along Rt. 422, 4 mi. N.E. of Portersville, 9/9/52, LKH and FHB.  
*C. stipata* Muhl. Awl-fruited Sedge  
*C. straminea* Willd. Straw-colored Sedge  
 Muddy Creek at Isle, 6/14/50, LKH and FHB.  
*C. stricta* Lam. Tussock Sedge  
 Bog, 1.5 mi. W. of West Liberty, 6/29/51, LKH and WEB.  
*C. swanii* (Fern.) Mackenz. Swan's Sedge  
*C. tribuloides* Wahlenb. Blunt Broom Sedge  
*C. tuckermani* Boott. Tuckerman's Sedge  
 Muddy Creek at Isle, 6/14/50, LKH and FHB.  
*C. vesicaria* L. Inflated Sedge  
 1 mi. above Girl Scout Camp on Connoquenessing Creek near Ribold, 7/28/28, JB.  
*\*C. vesicaria* var. *monile* (Tuckerm.) Fern.  
*C. virescens* Muhl. Ribbed Sedge  
 Portersville Station, 6/29/59, LKH and WEB.  
 2 mi. N.W. of Renfrew, 7/9/33, A. J. Deer.  
*C. vulpinoidea* Michx. Fox Sedge  
*C. woodii* Dew. Wood's Sedge  
 Lowrie Run near Emlenton, 5/24/25, JB.

#### *Cladium*

- C. mariscoides* (Muhl.) Torr. Twig Rush  
 Bog, 1.5 mi. W. of West Liberty, 7/10/65, WEB.



*Cyperus*

- C. rivularis* Kunth Shining Cyperus  
Near Ribold, 8/11/28, JB.  
*C. strigosus* L. Straw-colored Cyperus

*Dulichium*

- D. arundinaceum* (L.) Britt. Three-way Sedge

*Eleocharis*

- \**E. acicularis* (L.) R. & S. Needle Spike Rush  
*E. obtusa* (Willd.) Schultes Blunt Spike Rush  
*E. PAUCIFLORA* var. *fernaldii* Svenson Few-flowered Spike Rush  
In moist soil, Butler Reservoir, Rt. 38, N.E. of Butler, 11/30/49, LKH and OEJ.  
*E. smallii* Britt. Small's Spike Rush  
Adams, Glade Run, 8/28/26, JB.  
\**E. tenuis* (Willd.) Schultes Slender Spike Rush

*Rhynchospora*

- R. alba* (L.) Vahl White Beak Rush

*Scirpus*

- \**S. atrovirens* Willd. Dark Green Bulrush  
*S. atrovirens* var. *georgianus* (Harper) Fern. Georgia Bulrush  
*S. cyperinus* (L.) Kunth. Wool-grass  
*S. cyperinus* var. *pelius* Fern. Blackish Wool-grass  
Dutilh Church, on old Perry Highway, near Allegheny County line, 10/5/12, OEJ.  
*S. polyphyllus* Vahl. Leafy Bulrush  
*S. validus* var. *creber* Fern. Great Bulrush

## Family ARACEAE

*Acorus*

- A. calamus* L. Sweet Flag  
Muddy Creek, 1 mi. W. of Isle, 7/6/60, LKH.

*Arisaema*

- A. atrorubens* (Ait.) Blume Jack-in-the-pulpit  
*A. atrorubens* f. *viride* (Engelm.) Fern. Green-flowered Jack-in-the-pulpit  
*A. atrorubens* f. *zebrinum* (Sims) Fern. Purple-flowered Jack-in-the-pulpit  
*A. dracontium* (L.) Schott Green Dragon  
Muddy Creek, 1.5 mi. E. of Portersville, 6/6/61, LKH.  
\**A. pusillum* (Peck) Nash Small Jack-in-the-pulpit  
\**A. stewardsonii* Britt. Stewardson Brown's Indian Turnip

*Symplocarpus*

- S. foetidus* (L.) Nutt. Skunk Cabbage

## Family LEMNACEAE

*Lemna**L. minor* L.

Least Duckweed

*Spirodela**S. polyrrhiza* (L.) Schleid.

Water-flaxseed

Wolf Creek, N. of Slippery Rock, 8/13/22, OEJ.

*Wolffia**W. columbiana* Karst

Columbian Wolffia

Muddy Creek at Isle, 8/15/61, LKH.

## Family COMMELINACEAE

*Tradescantia**T. ohioensis* Raf.

Reflexed Spiderwort

Renfrew, 6/13/26, JB.

## Family JUNCACEAE

*Juncus**J. acuminatus* Michx.

Sharp-fruited Rush

*J. brachycephalus* (Engelm.) Buch.

Broad-headed Rush

Area with springs, across road from Butler Reservoir, 9 mi. N. of Butler, 9/26/53, WEB.

\**J. bufonius* L.

Toad Rush

*J. canadensis* J. Gay

Canada Rush

*J. debilis* Gray

Weak Rush

Ditch at Ribold, 8/31/28, JB.

*J. effusus* var. *pylpei* (Laharpe) Fern. and Wieg.

Pylaei's Soft Rush

*J. effusus* var. *solutus* Fern. and Wieg.

Loose Soft Rush

*J. marginatus* Rostk.

Grass-leaved Rush

*J. subcaudatus* (Engelm.) Coville and Blake

Tufted Rush

Buhl farm, 9/21/24, H. W. Graham.

4 mi. S.E. of Prospect, 10/17/53, LKH and WEB.

*J. tenuis* Willd.

Slender Rush

*Luzula**L. acuminata* Raf.

Hairy Wood Rush

*L. echinata* (Small) F. J. Herm.

Hedgehog Wood Rush

Brush Creek Swamp, N. of Warrendale, 6/5/09, OEJ.

*L. multiflora* (Retz.) Lejeune

Common Wood Rush

## Family LILIACEAE

*Allium**A. canadense* L.

Wild Garlic

*A. cernuum* Roth.

Nodding Wild Onion

*A. tricoccum* Ait.

Wild Leek

- Asparagus*
- A. OFFICINALE L. Garden Asparagus  
Near Marwood, 5/30/25, Mima Milliron. An escape.
- Chamaelirium*
- C. luteum* (L.) Gray Fairy Wand
- Clintonia*
- C. umbellulata* (Michx.) Morong White Clintonia
- Erythronium*
- E. albidum* Nutt. White Trout-lily  
*E. americanum* Ker. Yellow Trout-lily
- Lilium*
- L. canadense* L. Canada Lily  
*L. canadense* f. *rubrum* Britt. Red form of Canada Lily  
Jennings Blazing-star Prairie, at Stone House, 7/10/64, James Lovell.  
*L. canadense* var. *editorum* Fern. Upland Red Canada Lily  
*L. superbum* L. Turk's-cap Lily
- Maianthemum*
- M. canadense* Desf. False Lily-of-the-Valley
- Medeola*
- M. virginiana* L. Indian Cucumber Root
- Melanthium*
- M. hybridum* Walt. Crisped Bunchflower  
Slope of Thorn Creek Valley, about 3 mi. S.E. of Renfrew, 7/23/39, OEJ.  
Near Marwood, 1925, Elizabeth Milliron.  
*M. virginicum* L. Bunchflower  
Hazel thicket at Ribold, 8/11/28, JB.  
Ribold, 8/10/46, WEB.
- Ornithogalum*
- O. UMBELLATUM L. Star-of-Bethlehem  
1 mi. S. of Butler Reservoir, 9 mi. N. of Butler, 5/20/45, OEJ. An escape.
- Polygonatum*
- P. biflorum* (Walt.) Ell. Smooth Solomon's-seal  
*P. canaliculatum* (Muhl.) Pursh Giant Solomon's-seal  
*P. pubescens* (Willd.) Pursh Hairy Solomon's-seal
- Smilacina*
- S. racemosa* (L.) Desf. False Spikenard  
*S. racemosa* var. *cylindrata* Fern. Cylindrical False Spikenard
- Smilax*
- S. herbacea* L. Carrion-flower

- S. hispida* Muhl. Bristly Greenbrier  
*S. rotundifolia* L. Catbrier

*Stenanthium*

- S. gramineum* var. *robustum* (Wats.) Fern. Stout Stenanthium

*Trillium*

- T. erectum* L. Ill-scented Trillium  
*T. erectum* f. *albiflorum* R. Hoffm. White Ill-scented Trillium  
*T. grandiflorum* (Michx.) Salisb. Large-flowered Trillium  
*T. sessile* L. Sessile-flowered Trillium

*Uvularia*

- °*U. grandiflora* Sm. Large-flowered Bellwort  
*U. perfoliata* L. Perfoliate Bellwort  
*U. sessilifolia* L. Sessile-leaved Bellwort

*Veratrum*

- V. viride* Ait. False Hellebore

## Family DIOSCOREACEAE

*Dioscorea*

- D. villosa* L. Hairy Wild Yam

## Family AMARYLLIDACEAE

*Hypoxis*

- H. hirsuta* (L.) Coville Yellow Star-grass

## Family IRIDACEAE

*Iris*

- °*I. versicolor* L. Blue Flag

*Sisyrinchium*

- S. angustifolium* Mill. Stout Blue-eyed-grass

## Family ORCHIDACEAE

*Aplectrum*

- A. hyemale* (Muhl.) Torr. Puttyroot  
 Woods S. of Butler, Feb. 1900, W. H. Reed.

*Calopogon*

- C. pulchellus* (Salisb.) R. Br. Grass-pink  
 Bog, 1.5 mi. W. of West Liberty, 6/28/41, OEJ.

*Corallorhiza*

- C. maculata* Raf. Spotted Coralroot  
 Wolf Creek, 1-2 mi. S.W. of Christleys Mills, 10/2/65, LKH.  
 Powdermill Run, between Petersville and Renfrew, 7/22/24, H. W. Graham.



*Cypripedium*

- C. acaule* Ait. Pink Lady's-slipper  
 Along Rt. 268, just N. of Bruin, 5/31/48, WEB.  
*C. calceolus* var. *pubescens* (Willd.) Correll Large Yellow Lady's-slipper  
 Muddy Creek area, 1 mi. W. of Isle, 6/6/61, LKH.  
*C. reginae* Walt. Showy Lady's-slipper  
 Near Slippery Rock, 6/23/25, OEJ.

*Goodyera*

- G. pubescens* (Willd.) R. Br. Downy Rattlesnake-plantain

*Habenaria*

- H. flava* var. *herbiola* (R. Br.) Ames and Correll Pale-green Wood Orchid  
 Stone House, on Rt. 8, S. of Slippery Rock, 8/7/52, LKH and WEB.  
 Girl Scout Camp near Ribold Station, 7/28/28, JB.  
*H. lacera* (Michx.) Lodd. Ragged or Green-fringed Orchid  
*H. orbiculata* (Pursh) Torr. Round-leaved Orchid  
*H. psychodes* (L.) Spreng. Purple-fringed Orchid  
 Slippery Rock, 6/25/39, W. H. Hunt.

*Isotria*

- I. verticillata* (Willd.) Raf. Whorled Pogonia  
 2.2 mi. S. of Stone House, on Rt. 8, 5/22/65, WEB.

*Liparis*

- L. lilifolia* (L.) Richard Lily-leaved Twayblade

*Orchis*

- O. spectabilis* L. Showy Orchis  
 2 mi. below Christleys Mills, N. W. of Slippery Rock, 5/15/27, E. H. Graham.  
 Slippery Rock, May 1901, J. E. Winner.

*Spiranthes*

- S. cernua* (L.) Richard Nodding Ladies'-tresses  
*S. gracilis* (Bigelow) Beck Southern Slender Ladies'-tresses  
 Renfrew, 1/12/19, JB.

Class Dicotyledoneae  
 Family SALICACEAE

*Populus*

- P. ALBA* L. White Poplar  
 In yard near Mars, 9/10/10, J. B. Willson.  
 In yard, 4 mi. N.E. of Harmony, probably planted, Sept. 1925, LKH.  
*P. grandidentata* Michx. Large-toothed Aspen  
*P. tremuloides* Michx. Quaking Aspen

*Salix*

- S. alba* var. *vitellina* (L.) Stokes White Willow  
 4 mi. N.E. of Harmony, 1929, LKH. Probably planted.

<i>S. bebbiana</i> Sarg.	Long-beaked Willow
<i>S. discolor</i> Muhl.	Pussy Willow
<i>S. discolor</i> var. <i>latifolia</i> Anderss.	Broad-leaved Pussy Willow
Little Connoquenessing Creek, 1 mi. E. of Harmony, 4/18/15, OEJ.	
<i>S. FRAGILIS</i> L.	Crack Willow
<i>S. gracilis</i> var. <i>textoris</i> Fern.	Basket-maker's Willow
Bog, 1.5 mi. W. of West Liberty, 8/29/41, OEJ and CMB.	
<i>S. humilis</i> Marsh.	Gray Willow
<i>S. humilis</i> var. <i>hyporhysa</i> Fern.	Wrinkled Gray Willow
Bog, 1.5 mi. W. of West Liberty, 8/29/41, OEJ and CMB.	
<i>S. humilis</i> var. <i>microphylla</i> (Anderss.) Fern.	Dwarf Gray Willow
<i>S. interior</i> Rowlee	Sandbar Willow
<i>S. lucida</i> Muhl.	Shining Willow
<i>S. nigra</i> Marsh.	Black Willow
<i>S. rigida</i> Muhl.	Stiff Willow
<i>S. sericea</i> Marsh.	Silky Willow

## Family JUGLANDACEAE

*Carya*

<i>C. cordiformis</i> (Wang.) K. Koch	Bitternut Hickory
Upland woods, 4 mi. N.E. of Harmony, Sept. 1930, LKH.	
<i>C. ovalis</i> (Wang.) Sarg.	Sweet Pignut
Douthett to Dutilh Church, 10/5/12, OEJ.	
<i>C. ovata</i> (Mill.) K. Koch	Shagbark Hickory
<i>C. tomentosa</i> Nutt.	Mockernut Hickory

*Juglans*

<i>J. cinerea</i> L.	Butternut
<i>J. nigra</i> L.	Black Walnut

## Family BETULACEAE

*Alnus*

<i>A. rugosa</i> (DuRoi) Spreng.	Speckled Alder
Muddy Creek, 1 mi. W. of Isle, 9/14/60, LKH.	
<i>A. rugosa</i> var. <i>americana</i> (Regel) Fern.	Glaucous Alder
<i>A. rugosa</i> var. <i>americana</i> f. <i>hypomalaca</i> Fern.	Soft-leaved Glaucous Alder
Elliotts Mills, along Slippery Rock Creek, 8/17/22, OEJ.	
<i>A. serrulata</i> (Ait.) Willd.	Common Alder
<i>A. serrulata</i> var. <i>subelliptica</i> Fern.	Elliptic-leaved Alder
Ribold, 9/17/49, OEJ.	
Valencia, 9/27/04, OEJ.	

*Betula*

<i>B. lenta</i> L.	Sweet or Black Birch
* <i>B. lutea</i> Michx.	Yellow Birch

*Carpinus*

<i>C. caroliniana</i> var. <i>virginiana</i> (Marsh.) Fern.	Ironwood
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## Family CORYLACEAE

*Corylus*

*C. americana* Walt. Hazelnut

*Ostrya*

*O. virginiana* (Mill.) K. Koch Hop-hornbeam

## Family FAGACEAE

*Castanea*

*C. dentata* (Marsh.) Borkh. Chestnut

*Fagus*

*F. grandifolia* Ehrh. Beech

*Quercus*

*Q. alba* L. (incl. var. *latifolia*) White Oak

*Q. bicolor* Willd. Swamp White Oak

*Q. coccinea* Muenchh. Scarlet Oak

*Q. ilicifolia* Wang. Scrub Oak

*Q. imbricaria* Michx. Shingle Oak

*Q. x leana* (*Q. imbricaria* x *velutina*) Lea's Oak

Preston Reserve, 2 mi. W. of Butler, 8/6/47, F. W. Preston.

*Q. palustris* Muenchh. Pin Oak

*Q. prinoides* Willd. Dwarf Chestnut Oak

*Q. prinus* L. Chestnut Oak

*Q. rubra* L. Red Oak

*Q. velutina* Lam. Black Oak

## Family ULMACEAE

*Ulmus*

*U. americana* L. American Elm

*U. rubra* Muhl. Slippery Elm

## Family MORACEAE

*Morus*

*M. ALBA* L. White Mulberry

4 mi. N.E. of Harmony, 6/28/25, LKH. Escape or planted.

*M. rubra* L. Red Mulberry

4 mi. N.E. of Harmony, 6/28/25, LKH.

## Family CANNABINACEAE

*Humulus*

*H. lupulus* L. Common Hop

Ribold, 8/1/46, WEB.

## Family URTICACEAE

*Boehmeria*

*B. cylindrica* (L.) Sw. Bog Hemp

*Laportea**L. canadensis* (L.) Wedd.

Wood Nettle

*Pilea**P. pumila* (L.) Gray

Clearweed

*Urtica**U. gracilis* Ait.

Slender Nettle

## Family SANTALACEAE

*Comandra**C. umbellata* (L.) Nutt.

Bastard Toadflax

*C. richardsiana* Fern.

Richard's Bastard Toadflax

## Family ARISTOLOCHIACEAE

*Aristolochia**A. serpentaria* L.

Virginia Snakeroot

Jennings Blazing-star Prairie, at Stone House, intersection of Routes 8 and 78, 7/29/64, LKH.

0.5 mi. S. of Criders Corners, along Rt. 19, 7/19/45, LKH.

*Asarum**A. canadense* L.

Wild Ginger

## Family POLYGONACEAE

*Fagopyrum*\**F. sagittatum* Gilib.

Buckwheat

*Polygonum**P. arifolium* var. *pubescens* Fern.

Halberd-leaved Tearthumb

*P. AVICULARE* L.

Knotweed

\**P. coccineum* Muhl.

Muhlenberg's Knotweed

*P. coccineum* f. *terrestre* (Willd.) Stan.

Land form of Muhlenberg's Knotweed

Muddy Creek at Isle, 8/3/46, LKH.

*P. CONVOLVULUS* L.

Black Bindweed

\**P. hydropiper* L.

Common Smartweed

*P. hydropiperoides* Michx.

Mild Water Pepper

*P. lapathifolium* L.

Dock-leaved Smartweed

Near Ribold, 9/9/44, OEJ.

\**P. neglectum* Besser

Knotweed

*P. pensylvanicum* L.

Pinkweed

*P. pensylvanicum* var. *laevigatum* Fern.

Smooth Pinkweed

*P. PERSICARIA* L.

Lady's Thumb

*P. punctatum* var. *confertiflorum* (Meisn.) Fass.

Water Smartweed

*P. sagittatum* L.

Arrow-leaved Tearthumb

*P. scandens* L.

Climbing False Buckwheat



*Rumex*

- R. ACETOSELLA* L. Sheep-sorrel  
*R. altissimus* Wood Pale Dock  
 Near Buhl, 6/2/45, OEJ.  
*R. CRISPUS* L. Curled Dock  
*R. mexicanus* Meisn. Mexican Dock  
 Slippery Rock, Aug. 1920, S. H. Williams.  
*R. OBTUSIFOLIUS* L. Bitter Dock  
*R. orbiculatus* Gray Water Dock  
 Bog, 1.5 mi. W. of West Liberty, 8/28/41, OEJ.  
*R. verticillatus* L. Whorled Dock  
 Muddy Creek at Isle, 8/3/46, LKH.

*Tovara*

- T. virginiana* (L.) Raf. Jumpseed

## Family CHENOPODIACEAE

*Atriplex*

- A. patula* L. Orach  
 Near Ribold, 9/8/45, OEJ.  
*A. patula* var. *hastata* (L.) Gray Halberd-leaved Orach  
 Renfrew, 9/12/42, OEJ.  
 Buhl, 8/28/22, H. W. Graham.

*Chenopodium*

- C. ALBUM* L. Lamb's Quarters  
*C. BOTRYS* L. Feather-geranium  
 Near Ribold, 8/18/45, WEB.

*Salsola*

- S. kali* var. *TENUIFOLIA* Tausch Russian Thistle  
 Callery, 7/23/13, JB.

## Family AMARANTHACEAE

*Amaranthus*

- A. albus* L. Tumbleweed  
 4 mi. N.E. of Harmony, Sept. 1929, LKH.  
 \**A. HYBRIDUS* L. Green Amaranth  
*A. RETROFLEXUS* L. Rough Green Amaranth

## Family PHYTOLACCACEAE

*Phytolacca*

- P. americana* L. Pokeweed

## AIZOACEAE

*Mollugo*

- M. verticillata* L. Carpetweed

## Family PORTULACACEAE

*Claytonia**C. virginica* L.

Virginia Spring Beauty

## Family CARYOPHYLLACEAE

*Agrostemma**A. GITHAGO* L.

Corn Cockle

*Arenaria**A. lateriflora* L.

Blunt-leaved Sandwort

\**A. SERPYLLIFOLIA* L.

Thyme-leaved Sandwort

*Cerastium**C. nutans* Raf.

Nodding Mouse-ear Chickweed

*C. VULGATUM* L.

Common Mouse-ear Chickweed

*Dianthus**D. ARMERIA* L.

Deptford Pink

*D. BARBATUS* L.

Sweet William

Woods, Muddy Creek area, near Portersville Station, 6/26/62, LKH. An escape from cultivation.

*Lychnis**L. ALBA* Mill.

White Campion

*Myosoton**M. AQUATICUM* (L.) Moench.

Giant Chickweed

*Paronychia*\**P. canadensis* (L.) Wood

Smooth Forked Chickweed

*P. fastigiata* (Raf.) Fern.

Hairy Forked Chickweed

Plains Church, on Rt. 528, 9/17/24, OEJ.

*Saponaria**S. OFFICINALIS* L.

Bouncing-Bet

*S. VACCARIA* L.

Cowherb

Callery, 7/29/13, J. B. Willson.

*Silene**S. antirrhina* f. *deaneana* Fern.

Form of Sleepy Catchfly

Old railroad bed along Muddy Creek, at Isle, 6/14/50, LKH and FHB.

*S. caroliniana* var. *pensylvanica* (Michx.) Fern.

Wild Pink

Near Mars, May 1907, J. B. Willson.

*S. CUCUBALUS* Wibel

Bladder Campion

*S. NOCTIFLORA* L.

Night-flowering Catchfly

4 mi. N.E. of Harmony, July 1939, LKH.

*S. stellata* (L.) Ait. f.

Starry Campion

*S. stellata* var. *scabrella* (Nieuw.) Palm. and Stey.

Variety of Starry Campion

*S. virginica* L.

Fire Pink

*Stellaria*

<i>S. graminea</i> L.	Common Stitchwort
<i>S. longifolia</i> Muhl.	Long-leaved Stitchwort
<i>S. MEADIA</i> (L.) Cyrillo	Common Chickweed
<i>S. pubera</i> var. <i>silvatica</i> (Beguinet) Weath.	Wood Star-Chickweed
Near Ribold, 5/3/19, OEJ.	

## Family CERATOPHYLLACEAE

*Ceratophyllum*

<i>C. demersum</i> L.	Hornwort
Along Wolf Creek, N. of Slippery Rock, OEJ. No date.	
Slippery Rock Creek, W. of Slippery Rock, 9/30/47, Kenneth McDowell.	

## Family NYMPHAEACEAE

*Nuphar*

° <i>N. advena</i> (Ait.) Ait. f.	Yellow Pond-lily
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## Family RANUNCULACEAE

*Actaea*

<i>A. pachypoda</i> Ell.	Doll's-eyes
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*Anemone*

<i>A. canadensis</i> L.	Meadow Anemone
Brush Creek Swamp, N. of Warrendale, 6/5/09, OEJ.	
<i>A. quinquefolia</i> L.	Wood Anemone
<i>A. virginiana</i> L.	Tall Anemone

*Anemonella*

<i>A. thalictroides</i> (L.) Spach	Rue-anemone
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*Aquilegia*

<i>A. canadensis</i> L.	Columbine
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*Caltha*

<i>C. palustris</i> L.	Marsh Marigold
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*Cimicifuga*

<i>C. racemosa</i> (L.) Nutt.	Black Snakeroot
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*Clematis*

<i>C. virginiana</i> L.	Virgin's Bower
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*Delphinium*

<i>D. exaltatum</i> Ait.	Tall Larkspur
Ribold, 8/22/36, JB.	

*Helleborus*

- H. viridis* L. Green Hellebore  
Welsh bridge, along Little Connoquenessing Creek, 2 mi. W. of Connoquenessing,  
3/29/58, June Belles.

*Hepatica*

- H. acutiloba* D.C. Sharp-lobed Hepatica  
*H. americana* (D.C.) Ker. Round-leaf Hepatica  
*H. americana* f. *candida* Fern. White-flowered Hepatica  
Along Muddy Creek at Portersville Station, 5/3/62, LKH.

*Hydrastis*

- H. canadense* L. Goldenseal

*Ranunculus*

- R. abortivus* L. Kidney-leaf Buttercup  
*R. acris* L. Tall Buttercup  
*R. allegheniensis* Britt. Mountain Crowfoot  
*R. ambigens* Wats. Water-plantain Spearwort  
Near Ribold, 7/28/28, JB.  
*R. bulbosus* L. Bulbous Buttercup  
Slippery Rock, May 1901, J. E. Winner.  
*R. hispidus* Michx. Bristly Buttercup  
*R. hispidus* var. *falsus* Fern. Deceptive Buttercup  
*R. pensylvanicus* L. f. Bristly Crowfoot  
Bog, 1.5 mi. W. of West Liberty, 7/13/46, WEB.  
*R. recurvatus* Poir. Hooked Crowfoot  
*R. repens* L. Creeping Buttercup  
N. of Freeport, 5/11/46, WEB.  
Little Connoquenessing Creek at Mulligan Run, 8 mi. S.W. of Butler, 5/20/58,  
LKH and FHB.  
*R. repens* var. *glabratus* DC. Smooth Creeping Buttercup  
1.3 mi. N. of Marwood, 5/21/55, LKH.  
Little Connoquenessing Creek, 2 mi. S. of Connoquenessing, 5/20/58, LKH and  
FHB.  
Our only records in western Pennsylvania.  
*R. septentrionalis* Poir. Swamp Buttercup

*Thalictrum*

- T. dioicum* L. Early Meadow-rue  
*T. polygamum* Muhl. Tall Meadow-rue

## Family BERBERIDACEAE

*Berberis*

- B. thunbergii* DC. Japanese Barberry  
Frequent escape from cultivation.



*Caulophyllum**C. thalictroides* (L.) Michx.

Blue Cohosh

*Podophyllum**P. peltatum* L.

May-apple

*P. peltatum* f. *deamii* Raymond

Red-flowered form of May-apple

Epworth League woods, S. of Criders Corners at county line, 6/27/43, A. J. Deer and WEB.

## Family MAGNOLIACEAE

*Liriodendron**L. tulipifera* L.

Tulip Poplar

*Magnolia**M. acuminata* L.

Cucumber Tree

## Family ANNONACEAE

*Asimina**A. triloba* (L.) Dunal

Pawpaw

S. side of Buffalo Creek, 2-3 mi. N. of Freeport, 9/30/44, OEJ.

## Family LAURACEAE

*Lindera**L. benzoin* (L.) Blume

Spicebush

*Sassafras**S. albidum* (Nutt.) Nees

Sassafras

*S. albidum* var. *molle* (Raf.) Fern.

Red Sassafras

2 mi. W. of Slippery Rock, 7/22/57, Ethel Brubaker.

## Family PAPAVERACEAE

*Adlumia**A. fungosa* (Ait.) Greene

Allegheny Vine

McConnell's Mills, 7/16/25, E. H. McClelland.

*Chelidonium**C. majus* L.

Celandine

*Corydalis**C. flavula* (Raf.) DC.

Yellow Fumewort

Watson's Run, 2 mi. S. of Leasuresville, 5/8/40, LKH.

*Dicentra**D. canadensis* (Goldie) Walp.

Squirrel-corn

*D. cucullaria* (L.) Bernh.

Dutchman's Breeches

*Macleaya**M. cordata* (Willd.) R. Br.

Plume Poppy

1 mi. S. of Evans City, on Rt. 528, 8/5/46, LKH. An escape.

*Sanguinaria**S. canadensis* L.

Bloodroot

## Family CRUCIFERAE

*Alliaria**A. OFFICINALIS* Andrz.

Garlic-mustard

Camp Red Wing, Glade Run, N. of Valencia, 4/30/67, Fred Lochner.

*Arabis**A. canadensis* L.

Sicklepod

*A. glabra* (L.) Bernh.

Tower-mustard

Plains Church, on Rt. 528, 8/13/24, JB.

*A. laevigata* (Muhl.) Poir.

Smooth Rock-cress

*Armoracia**A. LAPATHIFOLIA* Gilib.

Horseradish

Along Muddy Creek, 1.5 mi. E. of Portersville Station, 6/6/61, LKH. Escape from cultivation.

*Barbarea**B. VULGARIS* R. Br.

Yellow Rocket

Galbraith farm near Mars, 5/23/10, J. B. Willson.

2 mi. N. of Connoquenessing, along creek, 8/20/22, E. H. Graham.

*B. VULGARIS* var. *ARCUATA* (Opiz.) Fries

Bow-fruited Yellow Rocket

*Brassica**B. KABER* var. *PINNATIFIDA* (Stokes) L. C. Wheeler

Crunchweed

Near Mars, 6/17/10, J. B. Willson.

*Capsella**C. bulbosa* (Schreb.) BSP.

Bulbous Cress

*Cardamine**C. BURSA-PASTORIS* (L.) Medic.

Shepherd's-purse

*C. douglassii* (Torr.) Britt.

Northern Bittercress

*C. pennsylvanica* Muhl.

Pennsylvania Bittercress

*C. rotundifolia* Michx.

Mountain Watercress

*Conringia**C. ORIENTALIS* (L.) Dumort.

Hare's-ear Mustard

*Dentaria**D. diphylla* Michx.

Crinkleroot

*D. heterophylla* Nutt.

Slender Toothwort

*D. laciniata* Muhl.

Cut-leaved Toothwort

*Hesperis**H. MATRIONALIS* L.

Dame's Rocket

Rt. 422, 2 mi. N.W. of Prospect, 10/5/50, LKH and FHB. Escape from cultivation.

*Lepidium**L. campestre* (L.) R. Br.

Field Peppergrass

*L. virginicum* L.

Poor-man's-Pepper

*Nasturtium**N. OFFICINALE* R. Br.

Watercress

*Rorippa**R. islandica* var. *fernaldiana* Butt. and Abbe

Marsh Cress

Muddy Creek at Isle, 7/15/46, LKH.

## Family DROSERACEAE

*Drosera**D. rotundifolia* L.

Round-leaved Sundew

Bog, 1.5 mi. W. of West Liberty, 8/29/41, OEJ and CMB.

## Family CRASSULACEAE

*Sedum**S. PURPUREUM* (L.) Link

Live-forever

*S. ternatum* Michx.

Mountain Stonecrop

## Family SAXIFRAGACEAE

*Chrysosplenium**C. americanum* Schwein.

Golden Saxifrage

*Heuchera**H. americanum* L.

Alumroot

*Hydrangea**H. arborescens* L.

Wild Hydrangea

*H. arborescens* var. *oblonga* T. and G.

Oblong-leaved Wild Hydrangea

*Mitella**M. diphylla* L.

Miterwort

*Parnassia**P. glauca* Raf.

Grass-of-Parnassus

Bog, 1.5 mi. W. of West Liberty, 9/14/41, OEJ.

*Penthorum**P. sedoides* L.

Ditch Stonecrop

*Ribes**R. americanum* Mill.

Wild Black Currant

*R. cynosbati* L.

Prickly Gooseberry

*R. glandulosum* Grauer

Skunk Currant

Bog, 1.5 mi. W. of West Liberty, 8/29/41, OEJ and CMB.

*R. SATIVUM* Syme

Garden Currant

An escape from cultivation.

*Saxifraga*

- S. pennsylvanica* L.  
*S. virginiana* Michx.

Swamp Saxifrage  
 Early Saxifrage

*Tiarella*

- T. cordifolia* L.

False Miterwort

## Family HAMAMELIDACEAE

*Hamamelis*

- H. virginiana* L.

Witch-hazel

## Family PLATANACEAE

*Platanus*

- P. occidentalis* L.

Sycamore

Near Mars, 9/1/09, J. B. Willson.

## Family ROSACEAE

*Agrimonia*

- A. gryposepala* Wallr.

Tall Hairy Agrimony

- A. parviflora* Ait.

Small-flowered Agrimony

- A. pubescens* Wallr.

Hairy Agrimony

- A. rostellata* Wallr.

Woodland Agrimony

N. edge of Zelienople, 7/3/44, LKH.

- A. striata* Michx.

Grooved Agrimony

Muddy Creek, 1.5 mi. E. of Portersville Station, 9/14/60, LKH.

Wolf Creek, N. of Slippery Rock, 8/13/22, OEJ.

*Amelanchier*

- A. arborea* (Michx. f.) Fern.

Shadbush

- A. intermedia* Spach

Swamp Sugar-Pear

Bog, 1.5 mi. W. of West Liberty, 6/29/51, LKH and WEB.

Muddy Creek at Isle, 6/14/50, LKH and FHB.

- A. laevis* Wieg.

Allegheny Shadbush

- A. spicata* (Lam.) K. Koch

Low Shadbush

Marwood, 6/7/40, Mima Milliron.

S. of Sarver, 5/10/33, E. H. McClelland.

*Aruncus*

- A. dioicus* (Walt.) Fern.

Goat's Beard

*Crataegus*

- C. biltmoreana* Beadle

Biltmore Thorn

Muddy Creek at Isle, 6/14/50, LKH and FHB.

- C. chrysocarpa* Ashe

Golden-fruited Thorn

Muddy Creek at Isle, 6/14/50, LKH and FHB.

- C. chrysocarpa* var. *phoenica* Palmer

Variety of Golden-fruited Thorn

Muddy Creek at Isle, 6/14/50, LKH and FHB.



- C. crus-galli* L. Cocksbur Thorn  
*C. disperma* Ashe Marshall's Thorn  
 Along creek, 2 mi. N. of Connoquenessing, 8/20/22, E. H. Graham.  
*C. macrosperma* Ashe Large-seeded Thorn  
*C. punctatus* Jacq. Dotted Thorn  
*C. uniflora* Muenchh. One-flowered Thorn  
 Jennings Blazing-star Prairie at Stone House, intersection of Routes 8 and 528,  
 7/29/64, LKH.

*Filipendula*

- F. rubra* (Hill) Robins Queen-of-the-Prairie  
 Ribold, 9/17/49, OEJ.

*Fragaria*

- F. vesca* L. Woodland Strawberry  
*F. vesca* f. *alba* (Ehrh.) Rydb. White-fruited Woodland Strawberry  
 Tributary of Glade Run, 2 mi. N.W. of Cooperstown, 7/2/46, LKH.  
 4 mi. N.E. of Harmony, roadbank outside yard, 6/9/25, LKH.  
*F. vesca* var. *americana* Porter American Woodland Strawberry  
 Mars, 1908, J. B. Willson.  
 Little Buffalo Creek at Monroe Station, 6/15/05, OEJ.  
*F. virginiana* Duchesne Scarlet Strawberry

*Geum*

- G. aleppicum* var. *strictum* (Ait.) Fern. Yellow Avens  
 Plains Church, 8/2/24, JB.  
*G. canadense* Jacq. White Avens  
*G. canadense* var. *grimesii* Fern. and Weath. Grime's Avens  
 Along creek, 2 mi. N. of Connoquenessing, 8/20/22, H. W. Graham.  
*G. laciniatum* Murr. Northern Rough Avens  
*G. rivale* L. Purple Avens  
 Near Slippery Rock, Wolf Creek, June 1901, J. E. Winner.  
*G. virginianum* L. Rough Avens

*Gillenia*

- G. trifoliata* (L.) Moench. Indian Physic

*Physocarpus*

- P. opulifolius* (L.) Maxim. Ninebark

*Potentilla*

- P. arguta* Pursh Tall Cinquefoil  
 Near Mars, 7/27/10, J. B. Willson.  
*P. canadensis* L. Dwarf Fivefinger  
*P. norvegica* L. Rough Cinquefoil  
*P. RECTA* L. Rough-fruited Cinquefoil  
*P. simplex* Michx. Old-field Cinquefoil

*Prunus*

- P. americana* Marsh. Wild Plum  
*P. AVIUM* L. Sweet Cherry  
*P. pennsylvanica* L. f. Fire Cherry  
*P. pumila* L. Sand Cherry  
 Railroad bank, N. of Freeport, Butler-Armstrong county line, 5/11/46, WEB.  
*P. serotina* Ehrh. Wild Black Cherry  
*P. virginiana* L. Choke Cherry

*Pyrus*

- P. arbutifolia* (L.) L. f. Red Chokeberry  
*P. coronaria* (L.) Mill. Wild Crab  
*P. coronaria* var. *lancifolia* (Rehd.) Fern. Narrow-leaved Wild Crab  
 Plains Church, on Rt. 528, 9/17/24, OEJ.  
*P. floribunda* Lindl. Purple Chokeberry  
 Bog, 1.5 mi. W. of West Liberty, 6/28/41, OEJ.  
*P. melanocarpa* (Michx.) Willd. Black Chokeberry

*Rosa*

- R. carolina* L. Pasture Rose  
*R. carolina* f. *glandulosa* (Crepin) Fern. Glandular form of Pasture Rose  
 2 mi. S.E. of Portersville, 8/4/53, LKH.  
*R. EGLANTERIA* L. Sweetbrier  
 Near Mars, 6/18/10, J. B. Willson. An escape from cultivation.  
*R. palustris* Marsh. Swamp Rose  
*R. WICHURIANA* Crepin Memorial Rose  
 Field, 2 mi. S.E. of Portersville, 8/4/53, LKH.

*Rubus*

- R. ajacens* Fern. Neighboring Blackberry  
 Muddy Creek at Isle, 6/14/50, LKH and FHB.  
*R. allegheniensis* Porter High-bush Blackberry  
*R. flagellaris* Willd. Northern Dewberry  
*R. hispidus* L. Swamp Dewberry  
*R. occidentalis* L. Black Raspberry  
*R. odoratus* L. Purple-flowering Raspberry  
*R. pubescens* Raf. Pubescent Blackberry  
 Muddy Creek, 1 mi. W. of Isle, 7/6/60, LKH.  
*R. rosa* Bailey Rose Blackberry  
 Brush Creek Swamp, N. of Warrendale, 6/5/09, OEJ.

*Sanguisorba*

- S. canadensis* L. Canadian Burnet  
 3 mi. S.E. of Slippery Rock, along creek, 9/17/44, OEJ.

*Sorbaria**S. SORBIFOLIA* (L.) A. Br.

False Spiraea

Portersville Station, along Muddy Creek, near old foundation, 4/27/54, Neil D. Richmond.

Anderson's Run, 2 mi. N.W. of Cooperstown, 1946, W. L. Black.

*Spiraea**S. alba* DuRoi

Meadowsweet

*S. tomentosa* L.

Hardhack

*Waldsteinia**W. fragarioides* (Michx.) Tratt.

Barren Strawberry

## Family LEGUMINOSAE

*Amphicarpa**A. bracteata* (L.) Fern.

Hog-peanut

*A. bracteata* var. *comosa* (L.) Fern.

Pitcher's Hog-peanut

*Apios**A. americana* Medic

Groundnut

*Baptisia**B. tinctoria* var. *crebra* Fern.

Wild Indigo

Field along Rt. 528, 1.5 mi. S. of junction with Rt. 8, 7/1/46, LKH.

*Cassia**C. hebecarpa* Fern.

Wild Senna

At Wolf Creek crossing of Rt. 108, 7/16/47, LKH and WEB.

Wolf Creek, N. of Slippery Rock, 8/13/22, OEJ.

*Desmodium**D. canadense* (L.) DC.

Canada Tick-trefoil

Pipestem School along Muddy Creek, 3 mi. E. of Mercer Road at Rt. 8, 8/2/41, OEJ.

\**D. canescens* (L.) DC.

Hoary Tick-trefoil

*D. cuspidatum* (Muhl.) Loud.

Large-bracted Tick-trefoil

*D. glutinosum* (Muhl.) Wood

Pointed-leaved Tick-trefoil

*D. nudiflorum* (L.) DC.

Naked-flowered Tick-trefoil

*D. paniculatum* (L.) DC.

Panicked Tick-trefoil

*D. perplexum* Schub.

Perplexing Tick-trefoil

*D. rotundifolium* DC.

Prostrate Tick-trefoil

*Lespedeza*\**L. capitata* Michx.

Round-headed Bush-clover

*L. hirta* (L.) Hornem.

Hairy Bush-clover

*L. intermedia* (S. Wats.) Britt.

Wand-like Bush-clover

*L. procumbens* Michx.

Trailing Bush-clover

Rt. 258, along Connoquenessing Creek, 2.5 mi. E. of Whitestown, 1/17/53, LKH and WEB.

- L. repens* (L.) Bart. Creeping Bush-clover  
 Rowan Station, 7/17/24, JB.  
*L. violacea* (L.) Pers. Violet Bush-clover  
*L. virginica* (L.) Britt. Slender Bush-clover  
 Rowan Station, 9/17/24, JB.  
 0.5 mi. S. of Mars, 8/26/45, WEB.

*Lotus*

- L. corniculatus* L. Birdsfoot Trefoil  
 Roadside along Findlay Run, at Pipestem Road, 3 mi. N.W. of West Sunbury,  
 9/11/69, LKH.

*Medicago*

- M. lupulina* L. Black Medic

*Melilotus*

- M. alba* Desr. White Sweet Clover  
*M. officinalis* (L.) Lam. Yellow Sweet Clover

*Phaseolus*

- P. polystachios* (L.) BSP. Wild Bean  
 McBride, 8/24/63, WEB.

*Robinia*

- R. pseudo-acacia* L. Black Locust

*Tephrosia*

- T. virginiana* (L.) Pers. Goat's Rue  
 Along Little Buffalo Creek at Windfield Junction, 10/12/40, OEJ.

*Trifolium*

- T. agrarium* L. Yellow or Hop Clover  
*T. hybridum* L. Alsike Clover  
*T. pratense* L. Red Clover  
*T. repens* L. White Clover  
*T. resupinatum* L. Persian Clover  
 Along Little Buffalo Creek N. of Freeport, 5/11/46, WEB. An escape from cultivation.

*Vicia*

- V. caroliniana* Walt. Wood Vetch  
*V. villosa* Roth Hairy Vetch

## Family LINACEAE

*Linum*

- L. striatum* Walt. Ridged Yellow Flax  
 Near Butler Reservoir, 9 mi. N. of Butler, 8/26/45, OEJ.  
 Bog, 1.5 mi. W. of West Liberty, 8/29/41, OEJ and CMB.



- L. USITATISSIMUM* L. Cultivated Flax  
 Callery, 7/27/13, JB. An escape from cultivation.  
*L. virginianum* L. Wild Yellow Flax

## Family OXALIDACEAE

*Oxalis*

- O. grandis* Small Great Yellow Wood-sorrel  
*O. stricta* L. Upright Yellow Wood-sorrel  
*O. violacea* L. Violet Wood-sorrel

## Family GERANIACEAE

*Geranium*

- G. carolinianum* L. Carolina Cranesbill  
 Little Buffalo Creek at Monroe Station, 6/17/05, OEJ.  
*G. maculatum* L. Wild Cranesbill  
*G. MOLLE* L. Dovesfoot Cranesbill  
 Slippery Rock, 7/13/40, A. G. Shields.

## Family POLYGALACEAE

*Polygala*

- P. paucifolia* Willd. Fringed Polygala  
 N. of Freeport, along Buffalo Creek, 5/11/46, WEB.  
*P. sanguinea* L. Purple Milkwort  
*P. verticillata* L. Whorled Milkwort  
*P. verticillata* var. *ambigua* (Nutt.) Wood Loose-spike Milkwort

## Family EUPHORBIACEAE

*Acalypha*

- A. rhomboidea* Raf. Rhombic Three-seeded Mercury  
*A. virginica* L. Virginia Three-seeded Mercury  
 Rowan, 8/22/31, JB.

*Euphorbia*

- E. corollata* L. Flowering Spurge  
*E. maculata* L. Eyebane  
*E. supina* Raf. Spotted Spurge  
*E. vermiculata* Raf. Hairy Spurge  
 McBride, 9/4/27, JB.  
 1 mi. above Ribold, 7/28/28, JB.

## Family CALLITRICHACEAE

*Callitriche*

- C. heterophylla* Pursh Large Water Starwort  
*C. palustris* L. Vernal Water Starwort  
 Muddy Creek at Mercer Road, Rt. 8, 9/5/40, OEJ.

## Family LIMNANTHACEAE

*Floerkea**F. proserpinacoides* Willd.

False Mermaid

## Family ANACARDIACEAE

*Rhus**R. copallina* var. *latifolia* Engler

Broad-leaved Dwarf Sumac

*R. glabra* L.

Smooth Sumac

*R. typhina* L.

Staghorn Sumac

*R. vernix* L.

Poison Sumac

Bog, 1.5 mi. W. of West Liberty, 9/16/40, LKH.

## Family AQUIFOLIACEAE

*Ilex**I. montana* (T. & G.) Gray

Mountain Holly

McConnell's Mills, 7/26/25, E. H. McClelland.

*I. verticillata* (L.) Gray

Winterberry

## Family CELASTRACEAE

*Celastrus**C. scandens* L.

Climbing Bittersweet

*Euonymus**E. americanus* L.

Strawberry-bush

Muddy Creek, just E. of Portersville Station, 9/22/62, WEB.

*E. atropurpureus* Jacq.

Wahoo

Woods along Sugar Creek, Oct. 1946, Sister Mary Clement.

\**E. obovatus* Nutt.

Running Strawberry-bush

## Family STAPHYLEACEAE

*Staphylea**S. trifolia* L.

Bladdernut

## Family ACERACEAE

*Acer**A. negundo* L.

Box-elder

Near Ribold, 9/9/44, OEJ.

*A. nigrum* Michx. f.

Black Maple

*A. rubrum* L.

Red Maple

*A. rubrum* var. *trilobum* K. Koch

Three-lobed Red Maple

4 mi. N.E. of Harmony, Sept. 1927, LKH.

*A. saccharinum* L.

Silver Maple

*A. saccharum* Marsh.

Sugar Maple

*A. spicatum* Lam.

Mountain Maple

Little Buffalo Creek, vicinity of Windfield Junction, 10/12/40, OEJ.

## Family BALSAMINACEAE

*Impatiens**I. capensis* Meerb.

Spotted Touch-me-not

*I. pallida* Nutt.

Pale Touch-me-not

## Family RHAMNACEAE

*Ceanothus**C. americanus* L.

New Jersey Tea

*Rhamnus**R. alnifolia* L'Her

Alder-leaved Buckthorn

Bog, 1.5 mi. W. of West Liberty, 6/28/41, OEJ.

## Family VITACEAE

*Parthenocissus**P. quinquefolia* (L.) Planch.

Virginia Creeper

*Vitis**V. aestivalis* Michx.

Summer Grape

*V. aestivalis* var. *argentifolia* (Munson) Fern.

Silver-leaf Grape

*V. labrusca* L.

Fox Grape

*V. riparia* Michx.

Riverbank Grape

1.5 mi. E. of Portersville Station, 6/26/62, LKH.

## Family TILIACEAE

*Tilia**T. americana* L.

Basswood

\**T. heterophylla* Vent.

White Basswood

## Family MALVACEAE

*Malva**M. neglecta* Wallr.

Cheeses

## Family GUTTIFERAE

*Hypericum**H. gentianoides* (L.) BSP.

Orange-grass

*H. mutilum* L.

Dwarf St. John'swort

*H. PERFORATUM* L.

Common St. John'swort

*H. punctatum* Lam.

Spotted St. John'swort

*H. spathulatum* (Spach) Steud.

Shrubby St. John'swort

\**H. virginicum* L.

Marsh St. John'swort

*H. virginicum* var. *fraserii* (Spach) Steud.

Fraser's Marsh St. John'swort

Bog, 1.5 mi. W. of West Liberty, 8/29/41, OEJ and CMB.

Petersville, 8/21/22, H. W. Graham.

## Family CISTACEAE

*Lechea*

- L. leggettii* Britt. and Holick Leggett's Pinweed  
 Dutlih Church, on Rt. 19, N. of Allegheny County line, 10/5/12, OEJ.  
*L. racemulosa* Lam. Oblong-fruited Pinweed

## Family VIOLACEAE

*Hybanthus*

- H. concolor* (T. F. Forst.) Spreng. Green Violet  
 Bear Run, 2-3 mi. N.N.E. of Bruin, 5/15/62, LKH and FHB.

*Viola*

- V. affinis* LeConte LeConte's Violet  
*V. blanda* Willd. Sweet White Violet  
*V. canadensis* L. Tall White Violet  
*V. conspersa* Reichenb. Dog Violet  
*V. x conturbata* House (*V. cucullata* x *V. sororia*) Violet hybrid  
 Muddy Creek at Portersville Station, 5/6/60, LKH.  
*V. cucullata* Ait. Marsh Blue Violet  
*V. cucullata* f. *albiflora* Britt. White form of Marsh Blue Violet  
 Bog, 2 mi. W. of West Liberty, 5/29/65, WEB.  
*V. x fernaldii* House (*sororia* x *V. fimbriatula*) Violet hybrid  
 Connoquenessing Creek at Ribold, 5/19/17, OEJ.  
*V. fimbriatula* Sm. Ovate-leaved Violet  
 \**V. hastata* Michx. Halberd-leaved Violet  
*V. hirsutula* Brainerd Southern Wood Violet  
*V. lanceolata* L. Lance-leaved Violet  
 Butler-Armstrong county line, along railroad, near Buffalo Creek, N. of Freeport,  
 5/11/46, WEB.  
*V. x napae* House (*V. papilionacea* x *V. sororia*) Violet hybrid  
 Muddy Creek at Portersville Station, 5/5/62, LKH.  
 1.3 mi. N. of Marwood, 5/21/55, LKH.  
*V. pallens* (Banks) Brainerd Eastern Sweet White Violet  
*V. palmata* L. Early Blue Violet  
 Near Mars, 5/10/10, JB.  
 Slippery Rock College, Apr. 1896, Sarah Marshall.  
*V. papilionacea* Pursh Meadow Blue Violet  
*V. pensylvanica* Michx. Smooth Yellow Violet  
 \**V. pensylvanica* f. *leiocarpa* (Fern. & Wieg.) Fern. Smooth-fruited Yellow Violet  
*V. priceana* Pollard Confederate Violet  
 Muddy Creek, 12 mi. W.N.W. of Butler on Rt. 422, 5/18/52, LKH.  
*V. primulifolia* var. *acuta* (Bigel) T. & G. Primrose-leaved Violet  
 Plains Church, S.E. of Evans City on Rt. 528, 8/31/09, OEJ.  
*V. pubescens* Ait. Downy Yellow Violet  
*V. rostrata* Pursh Long-spurred Violet  
*V. rostrata* x *striata* Brainerd Violet hybrid  
 Little Buffalo Creek at Monroe Station, 5/25/50, LKH and FHB.  
*V. sagittata* Ait. Arrow-leaved Violet



- V. sororia* Willd. Woolly Blue Violet  
*V. striata* Ait. Cream Violet  
*V. triloba* Schwein. Three-lobed Violet

## Family LYTHRACEAE

*Cuphea*

- C. petiolata* (L.) Koehne Clammy Cuphea  
 Portersville, 8/28/22, H. W. Graham.

*Lythrum*

- L. SALICARIA* L. Purple Loosestrife  
 Rt. 8, 0.75 mi. S. of McBride, 7/29/50, WEB. Escape.

## Family NYSSACEAE

*Nyssa*

- N. sylvatica* Marsh. Sour Gum  
*N. sylvatica* var. *caroliniana* (Poir.) Fern. Carolina Sour Gum

## Family ONAGRACEAE

*Circaea*

- C. alpina* L. Alpine Enchanter's Nightshade  
 2 mi. N. of Slippery Rock, 5/20/22, OEJ.  
*C. quadrisulcata* var. *canadensis* (L.) Hara Canadian 4-furrowed Enchanter's  
 Nightshade

*Epilobium*

- E. angustifolium* L. Fireweed  
*E. coloratum* Biehler Purple-leaved Willow Herb  
*E. glandulosum* var. *adenocaulon* (Haussk.) Fern. Northern Willow Herb

*Gaura*

- G. biennis* L. Biennial Gaura  
 Slippery Rock, Aug. 1920, S. H. Williams.

*Ludwigia*

- L. alternifolia* L. Seedbox  
*L. PALUSTRIS* var. *americana* (DC.) Fern. & Grisc. Water-purslane

*Oenothera*

- O. biennis* L. Common Evening-primrose  
*O. perennis* L. Small Sundrops  
*O. tetragona* var. *longistipata* (Pennell) Munz Common Sundrops

## Family HALORAGACEAE

*Proserpinaca*

- P. palustris* var. *crebra* Fern. and Grisc. Mermaid-weed  
 Muddy Creek along Rt. 422, 12 mi. W.N.W. of Butler, 9/14/51, LKH and FHB.  
 Muddy Creek at Isle, 6/14/50, LKH and FHB.

## Family ARALIACEAE

*Aralia*

- A. hispida* Vent. Bristly Sarsaparilla  
 Hillside just W. of Ribold, 6/14/58, WEB.  
*A. nudicaulis* L. Wild Sarsaparilla  
*A. racemosa* L. American Spikenard  
 \**A. spinosa* L. Hercules'-club

*Panax*

- P. quinquefolius* L. Ginseng  
 Slippery Rock, 6/23/25, OEJ. Because of widespread collecting for medicinal purposes, specimens of this species are rarely found.  
*P. trifolius* L. Dwarf Ginseng

## Family UMBELLIFERAE

*Angelica*

- A. atropurpurea* L. Purple-stemmed Angelica  
 Swampy meadow along Wolf Creek at crossing of Rt. 108, 7/16/47, LKH and WEB.  
 Bog, 1.5 mi. W. of West Liberty, 6/28/41, OEJ.  
*A. venenosa* (Greenway) Fern. Hairy Angelica

*Cicuta*

- C. bulbifera* L. Bulb-bearing Water-hemlock  
*C. maculata* L. Spotted Cowbane

*Cryptotaenia*

- C. canadensis* (L.) DC. Honewort

*Daucus*

- D. carota* L. Wild Carrot

*Erigenia*

- E. bulbosa* (Michx.) Nutt. Harbinger-of-spring  
 South side of Slippery Rock Creek, near Wolf Creek entrance, 0.5 mi. S.E. of Moore's Corner, 4/22/59, LKH and FHB.

*Heracleum*

- H. maximum* Bartr. Cow-parsnip  
 Roadside near Slippery Rock, 1934, M. E. Mathias.

*Hydrocotyle*

- H. americana* L. American Marsh Pennywort

*Osmorhiza*

- O. claytoni* (Michx.) C. B. Clarke Sweet Jarvil  
*O. longistylis* (Torr.) DC. Anise-root  
*O. longistylis* var. *villicaulis* Fern. Hairy-stemmed Anise-root

*Oxypolis*

- O. rigidior* (L.) C. & R. Water Dropwort  
 Bog, 1.5 mi. W. of West Liberty, 8/29/41, OEJ and CMB.

*Pastinaca*

- P. SATIVA* L. Parsnip

*Sanicula*

- S. canadensis* L. Short-styled Snakeroot  
*S. gregaria* Bickn. Clustered Snakeroot  
*S. marilandica* L. Black Snakeroot

*Taenidia*

- T. integerrima* (L.) Drude Yellow Pimpernel

*Thaspium*

- T. barbinode* (Michx.) Nutt. Hairy-jointed Meadow-parsnip  
*T. trifoliatum* var. *flavum* Blake Three-leaved Meadow-parsnip

*Zizia*

- Z. aptera* (Gray) Fern. Heart-leaved Alexanders  
 Plains Church, on Rt. 528, 9/17/24, OEJ.  
*Z. aurea* (L.) W.D.J. Koch Golden Alexanders

## Family CORNACEAE

*Cornus*

- C. alternifolia* L. f. Green Osier  
*C. ammomum* Mill. Red Willow  
*C. florida* L. Flowering Dogwood  
*C. obliqua* Raf. Silky Dogwood  
*C. racemosa* Lam. Racemose Dogwood

## Family PYROLACEAE

*Chimaphila*

- C. maculata* (L.) Pursh Spotted Wintergreen  
*C. umbellata* var. *cisatlantica* Blake Pipsissewa

*Monotropa*

- M. hypopithys* L. False Beechdrops  
*M. uniflora* L. Indian Pipe

*Pyrola*

- P. elliptica* Nutt. Shinleaf  
*P. rotundifolia* var. *americana* (Sweet) Fern. Round-leaved Wintergreen

## Family ERICACEAE

*Epigaea*

- E. repens* L. Trailing Arbutus

*Gaultheria*

*G. procumbens* L. Teaberry

*Gaylussacia*

*G. baccata* (Wang.) K. Koch Black Huckleberry

*Kalmia*

*K. latifolia* L. Mountain Laurel

*Lyonia*

*L. ligustrina* (L.) DC. Maleberry

*Rhododendron*

*R. maximum* L. Great Laurel

Northeastern part of county, Allegheny Twp., along Lowrey Run, near entrance to Allegheny River, 8/4/70, Fred Lochner.

*R. nudiflorum* (L.) Torr. Pinxter Flower

*R. nudiflorum* f. *glandulosum* (Porter) Fern. Glandular Pinxter Flower

\**R. roseum* (Loisel.) Rehd. Early Azalea

*Vaccinium*

*V. angustifolium* Ait. Low Sweet Blueberry

*V. angustifolium* var. *laevifolium* House Smooth-leaved Low Sweet Blueberry  
(= *V. lamarkii* Camp.)

0.5 mi. S. of Criders Corners, 7/19/45, LKH.

\**V. corymbosum* L. Highbush Blueberry

*V. macrocarpon* Ait. Large Cranberry

*V. stamineum* L. Deerberry

\**V. stamineum* var. *affine* (Ashe) Wherry Small Deerberry

*V. stamineum* var. *interius* (Ashe) Palmer and Steyer. Inland Deerberry

*V. stamineum* var. *neglectum* (Small) Deam Glauous-leaved Deerberry

Marwood, 5/30/25, M. R. Milliron.

*V. vacillans* Torr. Early Sweet Blueberry

## Family PRIMULACEAE

*Anagallis*

*A. arvensis* L. Scarlet Pimpernel

Slippery Rock, Aug. 1920, S. H. Williams.

*Dodecatheon*

*D. meadia* L. Shooting-star

Ribold, 5/16/14, JB.

*Lysimachia*

*L. ciliata* L. Fringed Loosetrife

*L. lanceolata* Walt. Lance-leaved Loosetrife

Plains Church, on Rt. 528, 8/2/24, JB.

0.5 mi. S. of Criders Corners, 7/19/45, LKH.



- L. NUMMULARIA* L. Moneywort  
*L. x producta* (Gray) Fern. Hybrid Loosestrife  
 Ribold, 7/24/13, JB.  
*L. quadrifolia* L. Whorled Loosestrife  
*L. terrestris* (L.) BSP. Swamp Loosestrife

*Samolus*

- S. parviflorus* Raf. Water-pimpernel  
 Swamp near Thorn Hill Industrial Home, 7/12/14, JB, Allegheny-Butler county line.

*Trientalis*

- T. borealis* Raf. Star Flower  
 Along Wolf Creek, 1.2 mi. S.W. of Christleys Mill, 5/22/65, LKH.

## Family EBENACEAE

*Diospyros*

- D. virginiana* L. Persimmon  
 Slippery Rock, 7/11/27, R. A. Waldron.

## Family OLEACEAE

*Fraxinus*

- F. americana* L. White Ash  
*F. nigra* Marsh. Black Ash  
*F. pensylvanica* var. *subintegerrima* (Vahl.) Fern. Green Ash  
 Muddy Creek at Isle, 6/26/62, LKH.

## Family GENTIANACEAE

*Bartonia*

- B. virginica* (L.) BSP. Yellow Bartonia  
 Bog, 1.5 mi. W. of West Liberty, 9/19/64, WEB.  
 Near Stone House, on Rt. 8, 4.5 mi. S.E. of Slippery Rock, 8/12/22, OEJ.

*Gentiana*

- G. andrewsii* Griseb. Closed Gentian  
*G. clausa* Raf. Blind Gentian  
*G. crinita* Froel. Fringed Gentian  
 Bog, 1.5 mi. W. of West Liberty, 9/14/41, OEJ.  
*G. flavida* Gray Yellowish Gentian  
 Ribold, 8/26/44, CMB and Max Henrici.

*Obolaria*

- O. virginica* L. Pennywort  
 Slippery Rock, May 1901, J. E. Winner.

*Sabatia*

- S. angularis* (L.) Pursh  
Near Mars, 8/2/09, J. B. Willson. Rose-pink

*Swertia*

- S. carolinensis* (Walt.) Ktze. American Columbo  
1 mi. N.W. of Slippery Rock, 8/24/32, Kellar Shelar.

## Family APOCYNACEAE

*Apocynum*

- A. androsaemifolium* L. Spreading Dogbane  
*A. cannabinum* L. Indian Hemp  
*A. cannabinum* var. *pubescens* (R.Br.) DC. Hairy Indian Hemp  
Yellow Creek, 3.5 mi. S.E. of Portersville, 7/25/44, LKH.  
*A. sibiricum* Jacq. Claspingleaved Dogbane  
Little Buffalo Creek, near Monroe Station, 6/26/38, JB.  
Field at Bovard, 8/7/52, LKH and WEB.

*Vinca*

- V. MINOR* L. Common Periwinkle  
An escape from cultivation.

## Family ASCLEPIADACEAE

*Asclepias*

- A. exaltata* L. Poke Milkweed  
*A. incarnata* L. Swamp Milkweed  
*A. quadrifolia* Jacq. Four-leaved Milkweed  
*A. syriaca* L. Common Milkweed  
*A. tuberosa* L. Butterfly Weed  
*A. viridiflora* var. *lanceolata* (Ives) Torr. Var. of Green Milkweed  
Rowan Station, "Harmony Line" car (abandoned interurban line), 8/12/28, JB.

## Family CONVULVULACEAE

*Convolvulus*

- C. sepium* L. White Hedge Bindweed  
North edge of Middle Lancaster, 7/15/68, LKH and Fred Lochner.  
*C. sepium* f. *coloratus* Lange Rose Hedge Bindweed  
*C. spithameus* L. Low Bindweed

*Cuscuta*

- C. gronovii* Willd. Gronovius's Dodder

## Family POLEMONIACEAE

*Phlox*

- P. divaricata* L. Blue Phlox  
*P. divaricata* f. *albiflora* Farw. White-flowered Blue Phlox  
Along Muddy Creek, 1.5 mi. E. of Portersville Station, 5/10/62, LKH.

*P. maculata* L.  
*P. paniculata* L.

Wild Sweet William  
 Perennial Phlox

*Polemonium*

*P. reptans* L.

Jacob's-ladder

Family HYDROPHYLLACEAE

*Hydrophyllum*

*H. virginianum* L.

Virginia Waterleaf

Family BORAGINACEAE

*Cynoglossum*

*C. OFFICINALE* L.  
*C. virginianum* L.

Common Hound's-tongue  
 Wild Comfrey

*Hackelia*

*H. virginiana* (L.) I. M. Johnston

Beggar's-lice

*Mertensia*

*M. virginica* (L.) Pers.

Virginia Bluebell

*Myosotis*

*M. laxa* Lehm.  
*M. SCORPIOIDES* L.  
*M. verna* Nutt.

Smaller Forget-me-not  
 True Forget-me-not  
 Spring Forget-me-not

Epworth League woods, S. of Criders Corners at county line, 6/5/52, LKH and WEB.

Family VERBENACEAE

*Lippia*

*L. lanceolata* Michx.

Frog Fruit

Along Little Connoquenessing Creek, 3 mi. N.E. of Harmony, Aug. 1944, LKH.

*Verbena*

*V. hastata* L.  
*V. urticifolia* L.

Blue Vervain  
 White Vervain

Family LABIATAE

*Agastache*

*A. nepetoides* (L.) Ktze.  
 Muddy Creek area, 8/20/62, LKH.

Yellow Giant Hyssop

*A. scrophulariaefolia* (Willd.) Ktze.

Purple Giant Hyssop

Along Muddy Creek, E. of Mercer Road on Rt. 8, 8/2/41, OEJ.

*Blephilia*

*B. ciliata* (L.) Benth.

Downy Blephilia

*Collinsonia*

*C. canadensis* L.

Richweed

*Cunila*

- C. origanoides* (L.) Britt. American Dittany  
 Anderson's Run, 2 mi. N.W. of Cooperstown, 9/5/46, LKH.  
 Watson's Run, 2 mi. S. of Leasuresville, Todd Sanctuary, 9/15/37, LKH.

*Glechoma*

- G. HEDERACEA L. Ground-ivy  
 G. HEDERACEA var. MICRANTHA Moricand Small-flowered Ground-ivy

*Hedeoma*

- H. pulegioides* (L.) Pers. American Pennyroyal

*Lamium*

- \**L. AMPLEXICAULE* L. Henbit  
*L. MACULATUM* L. Spotted Dead-nettle  
 Along Muddy Creek, 1 mi. W. of Isle, 6/21/61, LKH.  
 \**L. PURPUREUM* L. Purple Dead-nettle

*Leonurus*

- L. cardiaca* L. Motherwort

*Lycopus*

- L. americana* Muhl. American Bugleweed  
*L. uniflorus* Michx. Northern Bugleweed  
*L. virginicus* L. Virginia Bugleweed

*Meehania*

- M. cordata* (Nutt.) Britt. Meehania  
 Bear Run, about 4 mi. N. of Fairview (north of Petrolia), 6/18/61, Mrs. H. Schindler.

*Mentha*

- M. ALOPECUROIDES* Hull. Woolly Mint  
 Plains Church, on Rt. 528, 8/2/24, JB.  
*M. arvensis* var. *villosa* f. *glabrata* (Benth) Stewart Smooth form of Hairy Wild Mint  
 2 mi. N. of Slippery Rock, along Wolf Creek, 8/29/22, OEJ.  
*M. arvensis* var. *villosa* f. *typica* Stewart Hairy Wild Mint  
 Ribold, 8/10/46, WEB.  
 Butler Reservoir, 5 mi. N. of Butler, 9/29/51, WEB.  
*M. GENTILIS* L. Creeping Mint  
 Plains Church, on Rt. 528, 9/17/24, JB.  
*M. PIPERITA* L. Peppermint  
*M. ROTUNDIFOLIA* (L.) Huds. Round-leaved Mint  
 Ribold, 8/13/24, JB.  
*M. SPICATA* L. Spearmint



*Monarda*

<i>M. clinopodia</i> L.	Basil Balm
<i>M. didyma</i> L.	Oswego-tea
<i>M. fistulosa</i> L.	Wild Bergamot
<i>M. fistulosa</i> var. <i>mollis</i> (L.) Benth.	Soft Wild Bergamot
<i>M. media</i> Willd.	Purple Bergamot

*Nepeta*

<i>N. CATARIA</i> L.	Catnip
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*Prunella*

<i>P. VULGARIS</i> var. <i>lanceolata</i> (Bart.) Fern.	Heal-all
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*Pycnanthemum*

<i>P. tenuifolium</i> Schrad.	Slender-leaved Mountain-mint
<i>P. verticillatum</i> (Michx.) Pers.	Torrey's Mountain-mint
<i>P. virginianum</i> (L.) Durand and Jackson	Virginia Mountain-mint

*Satureja*

<i>S. vulgaris</i> var. <i>neogaea</i> Fern.	Dog-mint
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*Scutellaria*

<i>S. epilobifolia</i> A. Hamilton	Hooded Skullcap
Along Wolf Creek, at crossing of Rt. 108, 7/16/47, LKH and WEB.	
<i>S. incana</i> Biehler	Downy Skullcap
<i>S. lateriflora</i> L.	Mad-dog Skullcap
<i>S. parvula</i> var. <i>leonardi</i> (Epling) Fern.	Leonard's Skullcap
Plains Church, on Rt. 528, 8/13/24, JB.	

*Stachys*

<i>S. palustris</i> var. <i>homotricha</i> Fern.	Woundwort
Rt. 19, 0.5 mi. S. of Criders Corners, 7/19/45, LKH.	
Near Mars, 7/18/10, J. B. Willson.	

*Teucrium*

<i>T. canadense</i> var. <i>virginicum</i> (L.) Eat.	Wood-sage
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## Family SOLANACEAE

*Physalis*

<i>P. ALKEKENG</i> L.	Japanese Lantern
Near Marwood, 9/24/66, WEB. An escape from cultivation.	
<i>P. heterophylla</i> Nees	Clammy Ground-cherry
<i>P. virginiana</i> var. <i>subglabrata</i> (M. & B.) Waterfall	Smooth Ground-cherry
Plains Church, on Rt. 528, 9/17/22, JB.	

*Solanum*

<i>S. carolinense</i> L.	Horse-nettle
<i>S. DULCAMARA</i> L.	Bitter Nightshade

## Family SCROPHULARIACEAE

*Castilleja*

- C. coccinea* (L.) Spreng. Scarlet Painted-cup  
Connoquenessing Creek above Renfrew, 6/13/26, JB.

*Chelone*

- C. glabra* L. Smooth Turtlehead  
*C. glabra* var. *elatior* Raf. Pink Turtlehead  
*C. glabra* var. *linifolia* Coleman Flax-leaved Turtlehead  
Bog, 1.5 mi. W. of West Liberty, 9/14/41, OEJ.

*Collinsia*

- C. verna* Nutt. Blue-eyed Mary  
Near Mars, 5/14/49, Marion Scott.  
Slippery Rock, May 1921, S. H. Williams.

*Gerardia*

- G. flava* L. Smooth False Foxglove  
Ribold, 8/11/28, JB.  
Hilliards, 8/13/49, WEB.  
*G. flava* var. *macrantha* (Pennell) Fern. Large-flowered False Foxglove  
Ribold, 9/9/45, OEJ.  
*G. tenuifolia* Vahl. Slender Gerardia  
*G. virginica* (L.) BSP. Downy False Foxglove

*Gratiola*

- G. neglecta* Torr. Clammy Hedge-hyssop

*Linaria*

- L. vulgaris* Hill Butter-and-eggs

*Lindernia*

- L. dubia* (L.) Pennell False Pimpernel

*Mimulus*

- M. alatus* Ait. Sharp-winged Monkey Flower  
Ellitts Mills along Slippery Rock Creek, 8/19/22, OEJ.  
*M. ringens* L. Square-stemmed Monkey Flower

*Pedicularis*

- P. canadensis* L. Wood-betony  
*P. lanceolata* Michx. Swamp Lousewort  
4 mi. N.W. of West Sunbury, Hockenberry farm, 8/7/52, LKH and WEB.  
Bog, 1.5 mi. W. of West Liberty, 9/5/51, LKH and OEJ.

*Penstemon*

- P. digitalis* Nutt. Foxglove Beardtongue  
*P. hirsutus* (L.) Willd. Hairy Beardtongue

- P. laevigatus* Ait. Smooth Beardtongue  
 Pipestem School, along Muddy Creek, 3 mi. E. of Rt. 8, 8/2/41, OEJ.  
 Muddy Creek at Isle, 6/14/50, LKH and FHB.

*Scrophularia*

- S. lanceolata* Pursh Hare Figwort  
*S. marilandica* L. Carpenter's-square

*Verbascum*

- V. BLATTARIA* L. Moth Mullein  
*V. BLATTARIA* f. *ALBIFLORA* (Don) House White-flowered Moth Mullein  
 0.5 mi. W. of Middle Lancaster, along Scholars Run, 7/15/68, LKH and Fred  
 Lochner.  
*V. THAPSUS* L. Common Mullein

*Veronica*

- V. americana* (Raf.) Schwein American Brooklime  
*V. ARVENSIS* L. Corn Speedwell  
 Epworth League woods at Allegheny County line, N. of Warrendale, 5/5/46,  
 WEB.  
*V. officinalis* L. Common Speedwell  
 \**V. peregrina* L. Purslane Speedwell  
*V. scutellata* L. Marsh Speedwell  
 Slippery Rock, 6/23/25, OEJ.  
*V. SERPYLLIFOLIA* L. Thyme-leaved Speedwell

*Veronicastrum*

- V. virginicum* (L.) Farw. Culver's-physic

## BIGNONIACEAE

*Catalpa*

- C. speciosa* Warder Hardy Catalpa  
 Slippery Rock, 7/15/26, A. T. Cotton. (Shade tree on street.)

## Family OROBANCHACEAE

*Conopholis*

- C. americana* (L.) Wallr. Squawroot

*Epifagus*

- E. virginiana* (L.) Bart. Beechdrops

*Orobanche*

- O. uniflora* L. One-flowered Broomrape

## Family LENTIBULARIACEAE

*Utricularia*

- U. vulgaris* L. Common Bladderwort  
 Wolf Creek, 2 mi. N. of Slippery Rock, 8/8/22, OEJ.  
 Slippery Rock Creek, W. of Slippery Rock, 9/20/47, Kenneth McDowell.

## Family ACANTHACEAE

*Justicia**J. americana* (L.) Vahl

Water-willow

## Family PHRYMACEAE

*Phryma**P. leptostachya* L.

Lopseed

Near Mars, 7/11/20, J. B. Willson.

## Family PLANTAGINACEAE

*Plantago**P. aristata* Michx.

Bracted Plantain

Ribold, 7/27/13, JB.

*P. lanceolata* L.

English Plantain

\**P. major* L.

Common Plantain

*P. rugelii* Dcne.

Rugel's Plantain

\**P. virginica* L.

Dwarf Plantain

## Family RUBIACEAE

*Cephalanthus**C. occidentalis* L.

Buttonbush

*Galium**G. aparine* L.

Cleavers

*G. asprellum* Michx.

Rough Bedstraw

*G. boreale* L.

Northern Bedstraw

*G. circaezans* Michx.

Wild Licorice

*G. circaezans* var. *hypomalacum* Fern.

Hairy Wild Licorice

*G. concinnum* T. & G.

Shining Bedstraw

*G. lanceolatum* Torr.

Torry's Wild Licorice

*G. mollugo* L.

Wild Madder

Muddy Creek at crossing of Rt. 308, 7/28/46, OEJ.

*G. obtusum* Bigel

Stiff Marsh Bedstraw

*G. pilosum* Ait.

Hairy Bedstraw

\**G. tinctorium* L.

Clayton's Bedstraw

*G. triflorum* Michx.

Sweet-scented Bedstraw

*G. triflorum* var. *asprelliforme* Fern.

Wolf Creek, 1-2 mi. N. of Slippery Rock, 8/13/22, OEJ.

Rockdale Road and Thorn Creek, 1.5 mi. N. of Rockdale, 7/26/66, LKH.

*Houstonia**H. caerulea* L.

Bluets

*Mitchella**M. repens* L.

Partridge-berry



## Family CAPRIFOLIACEAE

*Diervilla**D. lonicera* Mill.

Bush Honeysuckle

*Lonicera**L. canadensis* Bartr.

Fly Honeysuckle

*L. dioica* var. *glaulescens* (Rydb.) Butters

Douglas' Honeysuckle

*Sambucus**S. canadensis* L.

Common Elder

*S. pubens* Michx.

Red-berried Elder

*Symphoricarpos**S. orbiculatus* Moench

Coralberry

Near Renfrew, 10/12/19, JB.

*Triosteum**T. aurantiacum* Bickn.

Wild Coffee

Edge of bog at West Liberty, 6/26/69, WEB.

*T. perfoliatum* L.

Tinker's-weed

*Viburnum**V. acerifolium* L.

Maple-leaved Viburnum

*V. alnifolium* Marsh.

Hobblebush

Plains Church, on Rt. 528, 8/31/09, OEJ.

*V. cassinoides* L.

Witherod

*V. lentago* L.

Nannyberry

*V. prunifolium* L.

Black-haw

*V. rafinesquianum* Schultes

Downy Arrow-wood

Brush Creek Swamp, N. of Warrendale, 6/5/09, OEJ.

*V. recognitum* Fern.

Arrow-wood

## Family VALERIANACEAE

*Valerianella**V. chenopodifolia* (Pursh) DC.

Lamb's-lettuce

*V. intermedia* Dyal

Intermediate Lamb's-lettuce

Glade Run, N. of Cooperstown, 5/23/26, JB.

## Family DIPSACACEAE

*Dipsacus**D. sylvestris* Huds.

Teasel

## Family CUCURBITACEAE

*Echinocystis**E. lobata* (Michx.) T. & G.

Wild Balsam-apple

*Sicyos*

- S. angulatus* L. Bur-cucumber  
Near Ribold, 9/9/44, OEJ.

## Family CAMPANULACEAE

*Campanula*

- C. americana* L. Tall Bellflower  
*C. aparinoides* Pursh Marsh Bellflower  
*C. RAPUNCULOIDES* L. European Bellflower  
*C. uliginosa* Rydb. Blue Marsh Bellflower  
Bog, 1.5 mi. W. of West Liberty, 6/28/41, OEJ and CMB.

*Lobelia*

- L. cardinalis* L. Cardinal Flower  
*L. cardinalis* f. *alba* (Eat.) St. John White form of Cardinal Flower  
Moraine State Park, near Isle, 8/25/65, Cyrilla J. Mansmann.  
*L. inflata* L. Indian-tobacco  
*L. kalmii* L. Kalm's Lobelia  
Bog, 1.5 mi. W. of West Liberty, 8/22/40, CMB.  
*Ibid.*, 9/5/51, OEJ and LKH.  
*L. siphilitica* L. Great Lobelia  
*L. spicata* var. *originalis* McVaugh Spiked Lobelia

*Specularia*

- S. perfoliata* (L.) A. DC. Venus's Looking-glass

## Family COMPOSITAE

*Achillea*

- A. MILLEFOLIUM* L. Common Yarrow  
*A. MILLEFOLIUM* f. *ROSEA* Rand & Redf. Pink Yarrow

*Actinomeris*

- A. alternifolia* (L.) DC. Yellow Ironweed

*Ambrosia*

- A. artemisiifolia* L. Common Ragweed  
*A. trifida* f. *integrifolia* (Muhl.) Fern. Entire-leaved Great Ragweed  
Elliotts Mills, along Slippery Rock Creek, 8/19/22, OEJ.

*Anaphalis*

- A. margaritacea* var. *intercedens* Hara Pearly Everlasting

*Antennaria*

- A. fallax* Greene  
Slippery Rock, May 1901, J. E. Winner.  
*A. neglecta* Greene Long-leaved Pussy's-toes  
Near Ribold, 5/15/20, JB.  
Slippery Rock Township, 4/14/35, S. K. Eastwood.  
*A. neodioica* Greene Smaller Pussy's-toes

*A. neodioica* var. *attenuata* Fern.

Floodplain of Muddy Creek, at Isle, 6/14/50, LKH and FHB.

*A. parlinii* Fern.

Parlin's Pussy's-toes

*A. plantaginifolia* (L.) Hook.

Plantain-leaved Pussy's-toes

### *Anthemis*

*A. COTULA* L.

Dog-fennel

### *Arctium*

*A. MINUS* (Hill.) Bernh.

Common Burdock

### *Aster*

*A. acuminatus* Michx.

Whorled Aster

Plains Church, 8/31/09, OEJ.

*A. cordifolius* L.

Blue Wood Aster

*A. divaricatus* L.

White Wood Aster

*A. divaricatus* var. *tenebrosus* (Burg.) Eat. and Grise Burgess's White Wood Aster

Woods along Connoquenessing Creek at Renfrew, 8/31/28, JB.

*A. infirmus* Michx.

Cornel-leaved Aster

Woods at Ribold, 8/11/28, JB.

\**A. laevis* L.

Smooth Aster

*A. lateriflorus* (L.) Britt.

Calico Aster

*A. lateriflorus* var. *angustifolius* Wieg.

Narrow-leaved Calico Aster

Bog, 1.5 mi. W. of West Liberty, 9/21/46, WEB.

Southeast corner of Cooperstown, 10/3/43, OEJ.

*A. lowrieanus* Porter

Lowrie's Aster

*A. lowrieanus* var. *lanceolatus* Porter

Lance-leaved Aster

*A. macrophyllus* L.

Large-leaved Aster

*A. macrophyllus* var. *ianthinus* (Burg.) Fern.

Glandless Large-leaved Aster

North-central part of county, 7/24/41, OEJ.

*A. novae-angliae* L.

New England Aster

*A. patens* Ait.

Pale Purple Aster

4 mi. N.E. of Harmony, Sept. 1930, LKH.

*A. patens* var. *phlogifolius* (Muhl.) Nees

Thin-leaved Purple Aster

4 mi. N.E. of Harmony, Sept. 1927, LKH.

Near Ribold, 9/9/44, OEJ.

*A. pilosus* Willd.

White Heath Aster

*A. pilosus* var. *demotus* Blake

Smooth Heath Aster

*A. prenanthoides* Muhl.

Crooked-stem Aster

*A. puniceus* L.

Purple-stem Aster

*A. sagittifolius* Wedem.

Arrow-leaved Aster

*A. sagittifolius* f. *hirtellus* (Lindl.) Shinnars

Marsh Arrow-leaved Aster

*A. schreberi* Nees

Schreber's Aster

*A. shortii* Hook.

Short's Aster

Glade Run (Adams Stop), near Cooperstown, 1926, OEJ.

*A. simplex* Willd.

White-panicked Aster

*A. simplex* var. *interior* (Wieg.) Cronq.

Small-flowered White-panicked Aster

Bog, 1.5 mi. W. of West Liberty, 9/14/41, OEJ.

- A. simplex* var. *ramosissimus* (T. & G.) Cronq. Most-branched White-panicked Aster

Little Connoquenessing Creek at Milligan Run, 8 mi. S.W. of Butler, 9/25/57, LKH.

Valencia, 9/27/09, OEJ.

- A. umbellatus* Mill. Flat-top Aster

- A. undulatus* L. Wavy-leaf Aster

- A. vimineus* Lam. Small White Aster

3 mi. S.E. of Slippery Rock along creek, 9/17/44, OEJ.

### *Bidens*

- B. cernua* L. Nodding Bur-marigold

- B. comosa* (Gray) Wieg. Leafy-bracted Beggar-ticks

- \**B. coronata* var. *tenuiloba* (Gray) Sherff Tickseed-sunflower

- B. frondosa* L. Beggar-ticks

- B. vulgata* Greene Tall Beggar-ticks

### *Cacalia*

- C. atriplicifolia* L. Pale Indian-plantain

- C. suaveolens* L. Sweet-scented Indian-plantain

### *Centaurea*

- C. JACEA* L. Brown Knapweed

- C. MACULOSA* Lam. Spotted Knapweed

Stone House, on Rt. 8 at junction of Rt. 528, 9/17/44, OEJ.

- C. VOCHINENSIS* Bernh. Tyrol Knapweed

McBride Station, on "Butler Short Line" (abandoned interurban car line), 7/23/25, JB.

### *Chrysanthemum*

- C. leucanthemum* L. Ox-eye Daisy

- C. leucanthemum* var. *pinnatifidum* Lecoq & Lamotte Cut-leaved Ox-eye Daisy

### *Cichorium*

- C. intybus* L. Chicory

4 mi. N.E. of Harmony, 8/23/25, LKH.

### *Cirsium*

- C. altissimum* (L.) Spreng. Tall Thistle

- C. ARVENSE* (L.) Scop. Canada Thistle

- C. discolor* (Muhl.) Spreng. Field Thistle

Plains Church, on Rt. 528, 9/17/24, JB.

- C. muticum* Michx. Swamp Thistle

- C. pumilum* (Nutt.) Spreng. Pasture Thistle

- C. VULGARE* (Savi.) Tenore Bull Thistle



*Coreopsis*

- C. lanceolata* L. Lance-leaved Coreopsis  
 S.E. of Cooperstown, 6/11/41, OEJ. Escaped into field.  
*C. tripteris* L. Tall Coreopsis  
*C. tripteris* var. *deamii* Standl. Deam's Tall Coreopsis

*Erechtites*

- E. hieracifolia* (L.) Raf. Fireweed

*Erigeron*

- E. annuus* (L.) Pers. Daisy Fleabane  
*E. canadensis* L. Horseweed  
*E. philadelphicus* L. Philadelphia Fleabane  
*E. pulchellus* Michx. Robin's-plantain  
*E. strigosus* Muhl. Whitetop

*Eupatorium*

- E. fistulosum* Barratt Purple-stemmed Joe Pye Weed  
 \**E. fistulosum* f. *truncatum* Jenn. Truncate Joe Pye Weed  
*E. maculatum* L. Spotted-stemmed Joe Pye Weed  
*E. perfoliatum* L. Boneset  
*E. purpureum* L. Green-stemmed Joe Pye Weed  
*E. rugosum* Houtt. White Snakeroot  
*E. sessilifolium* L. Upland Boneset  
 Ribold, 9/9/44, OEJ.

*Galinsoga*

- G. ciliata* (Raf.) Blake Quickweed

*Gnaphalium*

- G. obtusifolium* L. Common Everlasting  
*G. uliginosum* L. Low Cudweed

*Helenium*

- H. autumnale* L. Common Sneezeweed  
*H. nudiflorum* Nutt. Purple-headed Sneezeweed

*Helianthus*

- H. decapetalus* L. Thin-leaved Sunflower  
*H. divaricatus* L. Woodland Sunflower  
*H. giganteus* L. Giant Sunflower  
*H. laetiflorus* Pers. Showy Sunflower  
 Near Eau Claire, 9/27/41, J. Kosinski.  
*H. microcephalus* T. & G. Small Wood Sunflower  
*H. strumosus* L. Pale-leaved Sunflower  
*H. tuberosus* L. Jerusalem Artichoke

*Heliopsis**H. helianthoides* (L.) Sweet

Ox-eye

*Hieracium**H. AURANTIAECUM* L.

Orange Hawkweed

*H. FLORENTINUM* All.

King Devil

Along Little Buffalo Creek, at Monroe Station, 5/30/46, WEB.

*H. gronovii* L.

Gronovius's Hawkweed

Ribold, 6/28/36, JB.

\**H. paniculatum* L.

Panicled Hawkweed

*H. PRATENSE* Tausch.

Common Yellow Hawkweed

*H. scabrum* Michx.

Rough Hawkweed

*H. venosum* L.

Veined Hawkweed

*Hypochaeris**H. RADICATA* L.

Long-rooted Cat's-ear

*Inula**I. HELENIUM* L.

Elecampane

*Krigia**K. biflora* (Walt.) Blake

Dwarf Dandelion

*Lactuca**L. biennis* (Moench.) Fern.

Tall Blue Lettuce

*L. biennis* var. *aurea* Jenn.

Tall Yellow Lettuce

Valencia, 9/27/04, OEJ.

Leasuresville, 8/22/06, Mrs. H. W. Fisher.

*L. biennis* f. *integrifolia* (T. & G.) Fern.

Entire-leaved Tall Lettuce

Buhl farm, on Rt. 68, 9/21/24, H. W. Graham.

6 mi. S.W. of Butler, off Rt. 68, 9/19/62, LKH and WEB.

\**L. canadensis* L.

Arrow-leaved Lettuce

*L. canadensis* var. *longifolia* (Michx.) Fern.

Long-leaved Lettuce

*L. canadensis* var. *obovata* Wieg.

Obovate-leaved Lettuce

4 mi. N.E. of Harmony, 5/8/37, LKH.

*L. SCARIOLA* L.

Prickly Lettuce

Muddy Creek, along Rt. 422, 12 mi. W. of Butler, 9/19/51, LKH and FHB.

*Leontodon**L. LEYSSERI* (Wallr.) G. Beck

Hairy Hawkbit

Muddy Creek, just E. of Portersville Station, 9/22/62, WEB.

*Liatris**L. spicata* (L.) Willd.

Blazing-star

*L. spicata* f. *albiflora* Britt.

Whiteflowered Blazing-star

Hockenberry farm, 3.5 mi. N.W. of West Sunbury, 8/11/66, William F. Kummer.

*Prenanthes*

- P. alba* L. White Rattlesnake Root  
*P. altissima* L. Tall Rattlesnake Root  
*P. trifoliolata* (Cass.) Fern. Call-of-the-Earth

*Rudbeckia*

- R. hirta* L. Black-eyed Susan  
*R. hirta* var. *pulcherrima* Farw. Beautiful Black-eyed Susan  
*R. laciniata* L. Tall Coneflower  
*R. speciosa* Wenderoth Showy Coneflower  
 Edge of Mars, 7/30/22, E. H. McClelland.  
 \**R. triloba* L. Thin-leaved Coneflower

*Senecio*

- S. aureus* var. *gracilis* (Pursh) Wood Slender Golden Ragwort  
*S. aureus* var. *intercurus* Fern. Golden Ragwort  
*S. obovatus* Muhl.  
 Thorn Creek, off Rt. 8, S.E. of McBride, 5/31/47, Mrs. Elliott Mason.

*Silphium*

- S. trifoliatum* L. Whorled Rosinweed

*Solidago*

- S. altissima* L. Tall Goldenrod  
*S. bicolor* L. White Goldenrod  
*S. caesia* L. Blue-stem Goldenrod  
*S. caesia* f. *axillaris* (Pursh) House Axillary-flowered Blue-stem Goldenrod  
*S. canadensis* L. Canada Goldenrod  
*S. flexicaulis* L. Zigzag Goldenrod  
*S. gigantea* Ait. Late Goldenrod  
*S. gigantea* var. *leiophylla* Fern. Smooth-leaved Late Goldenrod  
 Douthett to Dutilh Church, 10/5/12, OEJ.  
*S. graminifolia* (L.) Salisb. Grass-leaved Goldenrod  
*S. graminifolia* var. *nuttallii* (Greene) Fern. Nuttall's Goldenrod  
*S. juncea* Ait. Early Goldenrod  
*S. nemoralis* Ait. Old-field Goldenrod  
*S. patula* Muhl. Rough-leaved Goldenrod  
*S. rugosa* Ait. Wrinkle-leaved Goldenrod  
*S. rugosa* var. *aspera* (Ait.) Fern. Rough Wrinkle-leaved Goldenrod  
*S. speciosa* Nutt. Showy Goldenrod  
*S. squarrosa* Muhl. Stout Ragged Goldenrod  
*S. uliginosa* var. *linoides* (T. & G.) Fern. Marsh Goldenrod  
 Bog, 1.5 mi. W. of West Liberty, 9/14/41, OEJ.  
*S. ulmifolia* Muhl. Elm-leaved Goldenrod  
*S. ulmifolia* x *S. rugosa* var. *aspera* Ait. Goldenrod hybrid

*Sonchus*

- S. ASPER* (L.) Hill Spiny-leaved Sow-thistle

*Tanacetum*

- T. VULGARE* L. Common Tansy  
 North-central part of county, near Boyer, 9/19/43, OEJ.  
 Along Rt. 8, south-central part of county, 8/24/20, Marie Knauz.

*Taraxacum*

- T. ERYTHROSPERMUM* Andrz. Red-seeded Dandelion  
 Valencia, 9/27/04, OEJ.  
 Petersville, 8/24/22, H. W. Graham.  
*T. OFFICINALE* Weber Common Dandelion

*Tussilago*

- T. FARFARA* L. Coltsfoot

*Vernonia*

- V. altissima* Nutt. Tall Ironweed  
*V. noveboracensis* (L.) Michx. New York Ironweed

*Xanthium*

- X. chinense* Mill. Common Cocklebur  
 Buhl farm, on Rt. 528, 8/29/22, H. W. Graham.  
 Franklin Road Station, near Plains Church on Rt. 528, 9/27/24, JB.  
*X. italicum* Mor. Italian Cocklebur  
 Plains Church, on Rt. 528, 9/17/24, OEJ.

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PALEONTOLOGY AND GEOLOGY OF THE  
BADWATER CREEK AREA, CENTRAL WYOMING

## Part 7. Rodents of the Family Ischyromyidae

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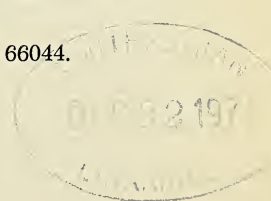
## INTRODUCTION

All ischyromyids described in this report are from the Tepee Trail formation and are of late Eocene age. Nine species of ischyromyids are recognized as occurring at one or more of six different localities within the Tepee Trail formation. Approximately 180 isolated teeth, one jaw with P<sup>1</sup>-M<sup>2</sup>, and two maxillary fragments with two or three teeth form the basis for the present study. One genus of ischyromyid, *Microparamys*, is not considered in the Systematic Review of this report, but is discussed by Mary Dawson in Part 8 of this series. In all, there are nine species of ischyromyids belonging to at least six, and possibly seven, genera.

As always when dealing with a sample composed primarily of isolated teeth, there is considerable risk of error in determining which deciduous premolars and permanent premolars are associated with which molars, and in deciding which upper molars are associated with which lower molars. This problem is less difficult when the isolated teeth from single localities only are considered at one time. No more than five species of ischyromid are known from any one locality in the Tepee Trail formation. Difference in size and in morphology between these five species at any locality has made it possible to separate and recognize taxonomic groups with some certainty. In some cases, e.g., *Leptotomus guildayi*, a considerable amount of variation is recognized for one species. This procedure is considered preferable to recognizing a number of different variants, or species, of a single genus as occurring at one locality. In several cases, only tentative generic assignments have been given, and in two in-

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stances, I have not named new species because the material does not allow for an adequate description of either population.

The association of upper and lower cheek teeth referred to any one species at any single locality is based upon the following assumptions:

1. That, as a number of tons of mudstone have been processed from localities 5, 5A, 6, and Wood, a representative sample of all species preserved at each locality has been obtained.
2. That at each locality there is only a single species in any one size-group exhibiting the same morphology (see Table 1.).
3. That the upper and lower teeth of similar size and similar morphology belong to the same species.. If this is not so, then there would be one species based upon upper teeth alone and another species based upon lower teeth alone.

Abbreviations used in this paper are: ACM, Amherst College Museum; CM, Carnegie Museum; LACM (CIT), Los Angeles County Museum (California Institute of Technology collection); UCM, University of Colorado Museum; a-p, anterior posterior; tr, transverse width (two measurements, the first of which is the width of the upper teeth or the anterior width of the lower teeth, and the second, the posterior width of the lower teeth); N, number; OR, observed range; M, mean; R, Rodent locality; W, Wood locality.

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#### CLASSIFICATION

I have given my reasons elsewhere (Black, 1968a) for including within the Family Ischyromyidae all rodents considered by Wood (1962) to belong to the Family Paramyidae. In working up the late Eocene ischyromyids from Badwater, it has been necessary to review all late Eocene ischyromyid material as well as to make a brief survey of all members of the family. This study does not review (and it would not be feasible to do

so here) all the rodent material that Wood (1962) studied and reported on in such comprehensive detail. However, during the course of this study a number of changes have had to be made in taxonomic assignments of late Eocene ischyromyid material. This, in turn, has led to a re-evaluation of the classification of all rodents here considered to be members of the Family Ischyromyidae.

The classification proposed below and followed in this paper is similar in some regards to those of Simpson (1945) and Wilson (1949). It differs from those two classifications in recognizing as distinct the families Sciuravidae and Cylindrodontidae, both of which Wilson and Simpson considered subfamilies within the family Ischyromyidae. Reasons for recognizing these families, given in an early paper (Black, 1968a), are based primarily on the major radiations seen in each of the two groups, radiations that depart markedly from the morphological pattern seen in members of the family Ischyromyidae.

#### Family Ischyromyidae Alston, 1876

Cheek teeth basically low-crowned and tritubercular with hypocone, when present, secondary in importance to protocone; lophate condition rare, found only in a few advanced forms; talonid basins generally large and undivided; infraorbital foramen generally small, rounded, not compressed; zygoma heavy; masseter arises from ventral surface of zygoma; skull quite narrow in postorbital region; nasals usually long; temporal fossa large; brain case small, not inflated; bulla coossified only in a few species; tibia and fibula separate; humerus with entepicondylar foramen.

#### Subfamily Ischyromyinae Schlosser, 1911

U. Eoc.—U. Oligo., N.A.

Most advanced group in family; partially to completely lophate cheek teeth; four crests developed in upper and lower cheek teeth; hypocone distinct but subordinate to protocone; no mesoconid or mesostylid; hypolophid well developed.

#### Subfamily Paramyinae Simpson, 1945.

U. Paleo.—?L. Oligo., N.A.; L. Eoc.—

U. Eoc. Eur.; U. Eoc., L. Oligo.,

As.

Least specialized group in family; medium-to-large-sized rodents; cheek teeth generally simple in pattern, particularly in largest forms; enamel of cheek teeth often finely wrinkled to rugose; hypocones when present are small; mesoconids and mesostylids usually absent; entoconids generally continuous with posterolophids; anterior cingula of lower cheek teeth short.

#### Subfamily Reithroparamyinae Wood, 1962

L. Eoc.—U. Eoc., N.A.; L. Eoc.—M.

Eoc., Eur.

Small-to-medium-sized rodents; cheek teeth tending to become more complex;

hypocone usually present and large; mesoconid generally present; mesostylid small to absent; entoconid usually separated from posterolophid; anterior cingulum of lower cheek teeth elongate; short hypolophid crest commonly present.

Subfamily Prosciurinae Wilson, 1949

U. Eoc.—L. Mio., N.A.; M.—U. Oligo., Eur.; U. Oligo., As.

Small-to-medium-sized rodents; cheek teeth moderately complex; hypocone absent or small; mesoconid large; mesostylid commonly crested; entoconid often separated from posterolophid; trigonid basin reduced; anterior cingulum quite short; hypolophid always present.

Order Rodentia Bowdich, 1821

Suborder Sciuromorpha Brandt, 1855

Superfamily Ischyromyoidae Wood, 1937

Family Ischyromyidae Alston, 1876

U. Paleo. L. Mio.

Subfamily Ischyromyinae Schlosser, 1911

*Ischyromys* Leidy, 1856.

[Including *Titanotheriomys* Matthew, 1910.]

U. Eoc.—?U. Oligo., N.A.

Subfamily Paramyinae Simpson, 1945

*Paramys* Leidy, 1871.

U. Paleo.—M. Eoc., N.A., L. Eoc., Eur.

*Leptotomus* Matthew, 1910.

[Including *Tapomys*<sup>1</sup> Wood, 1962.]

L.—U. Eoc., N.A.

*Thisbemys* Wood, 1959.

M.—U. Eoc., N.A.

*Ischyrotomus* Matthew, 1910.

M.—U. Eoc., N.A.

*Pseudotomus* Cope, 1872.

L.—M. Eoc., N.A.

*Manitsha* Simpson, 1941.

?L. Oligo., N.A.

*Mytonomys* Wood, 1956.

U. Eoc., N.A.

<sup>1</sup>For discussion of this synonymy see *Tapomys* in Systematic Review.

*Rapamys* Wilson, 1940.

U. Eoc., N.A.

*Pseudoparamys* Michaux, 1964.

L. Eoc., Eur.

*Plesiarctomys* Bravard, 1850.

M.-U. Eoc., Eur.

*Hulgana* Dawson, 1968.

L. Oligo., As.

#### Subfamily Reithroparamyinae Wood, 1962

*Reithroparamys* Matthew, 1920.

[Including *Uriscus*<sup>2</sup> Wood, 1962.]

L.-U. Eoc., N.A.

*Franimys* Wood, 1962.

L. Eoc., N.A.

*Microparamys* Wood, 1959.

L.-U. Eoc., N.A.; L.-M. Eoc., Eur.

*Lophiparamys* Wood, 1962.

L. Eoc., N.A.

*Janimus* Dawson, 1966.

U. Eoc., N.A.

#### Subfamily Prosciurinae Wilson, 1949

*Cedromus* Wilson, 1949.

M. Oligo., N.A.

*Pelycomys* Galbreath, 1953.

L.-M. Oligo., N.A.

*Prosciurus* Matthew, 1903.

L.-Oligo.—L. Mio., N.A.

*Spurimus*, new genus.

U. Eoc., N.A.

*Plesispermophilus* Filhol, 1883.

M.-U. Oligo., Eur.; U. Oligo., As.

#### Ischyromyidae *incertae sedis*

*Dectiadapis* Lemoine, 1891.

L. Eoc., Eur.

<sup>2</sup>The type, and only known specimen, of *Uriscus* is a lower jaw (LACM; CIT 2194) with worn M<sub>1</sub>-M<sub>3</sub>. The dental pattern is similar to that of *Reithroparamys gidleyi*. Because of its small size the California specimen probably represents a distinct species of *Reithroparamys*, *R. californicus*.



*Ailuravus* Rüttimeyer, 1891.

M. Eoc., Eur.

*Maurimontia* Stehlin and Schaub, 1951.

M. Eoc., Eur.

*Meldimys* Michaux, 1964.

L. Eoc., Eur.

## SYSTEMATIC REVIEW

### Order Rodentia

### Family Ischromyidae

### *Leptotomus guildayi*<sup>1</sup>, new species

### Figures 1-12

?*Rapamys* sp., Wood, 1949a, :557; ?*Rapamys* sp. B., Wood, 1962 :153.

TYPE: CM 14627, LM<sub>3</sub>.

HYPODGM: Type and P<sup>4</sup>, CM 14621, 15347, 15353, 18230; DP<sup>4</sup>, CM 16065; M<sup>1</sup> or <sup>2</sup>, CM 14620, 14625, 15339, 15343, 15349, 15350, 16064, 16068, 18235, 18238, 21980; M<sup>3</sup>, CM 14622, 15346, 19774; P<sub>4</sub>, 14626, 15342, 16769, 18231, UCM 24793; M<sub>1</sub> or <sub>2</sub>, CM 14628, 15340, 15341, 16067, 16770, 18197, 18227, 21976-21979, UCM 24739; M<sub>3</sub>, CM 16066-16068, 16767, 16768, 18234, UCM 24722, ACM 10014.

DISTRIBUTION: Type from Rodent locality (Black and Dawson, 1966, fig. 1). All other specimens from either Rodent or Wood locality. The Amherst College specimen (Wood, 1949a; 1962:153) is from the Wood locality.

DIAGNOSIS: Protoconid of P<sub>4</sub> crowded backwards and lingually into metaconid; hypolophid complete on P<sub>4</sub>-M<sub>3</sub> but generally low, not as strong as in *Ischyromys*, but better developed than in *Rapamys*; trigonid basins of M<sub>1</sub>-M<sub>3</sub> generally large, shallow, closed by strong metalophids; buccal valley wide on M<sub>1</sub>-M<sub>3</sub>; no mesoconid; hypocone distinct on M<sup>1</sup>-M<sup>2</sup>, absent on P<sup>4</sup>; single metaconules on P<sup>4</sup>-M<sup>3</sup>; anterior cingulum short on P<sup>4</sup>-M<sup>3</sup>.

DESCRIPTION: There is only one tooth that appears to be a deciduous upper premolar, CM 16065 (fig. 1). This tooth is slightly smaller than the permanent P<sup>4</sup> and displays a distinct hypocone, which is not present on P<sup>4</sup>. The metaconule of dP<sup>4</sup> is as large as the metacone; it is connected to the internal face of the protocone near its base. There is a distinct protoconule on dP<sup>4</sup> and a large mesostyle. The anterior cingulum of dP<sup>4</sup> is wider than that of P<sup>4</sup>.

The permanent fourth premolars are triangular in occlusal outline (figs. 2 and 3) with high, rather sharp protocones, but no hypocones. The anterior cingula are wider than the posterior, and curve back into the anterior slopes of the paracones. The metaconules are very large, possibly more bulbous than the metacones. There is no distinct metaloph on

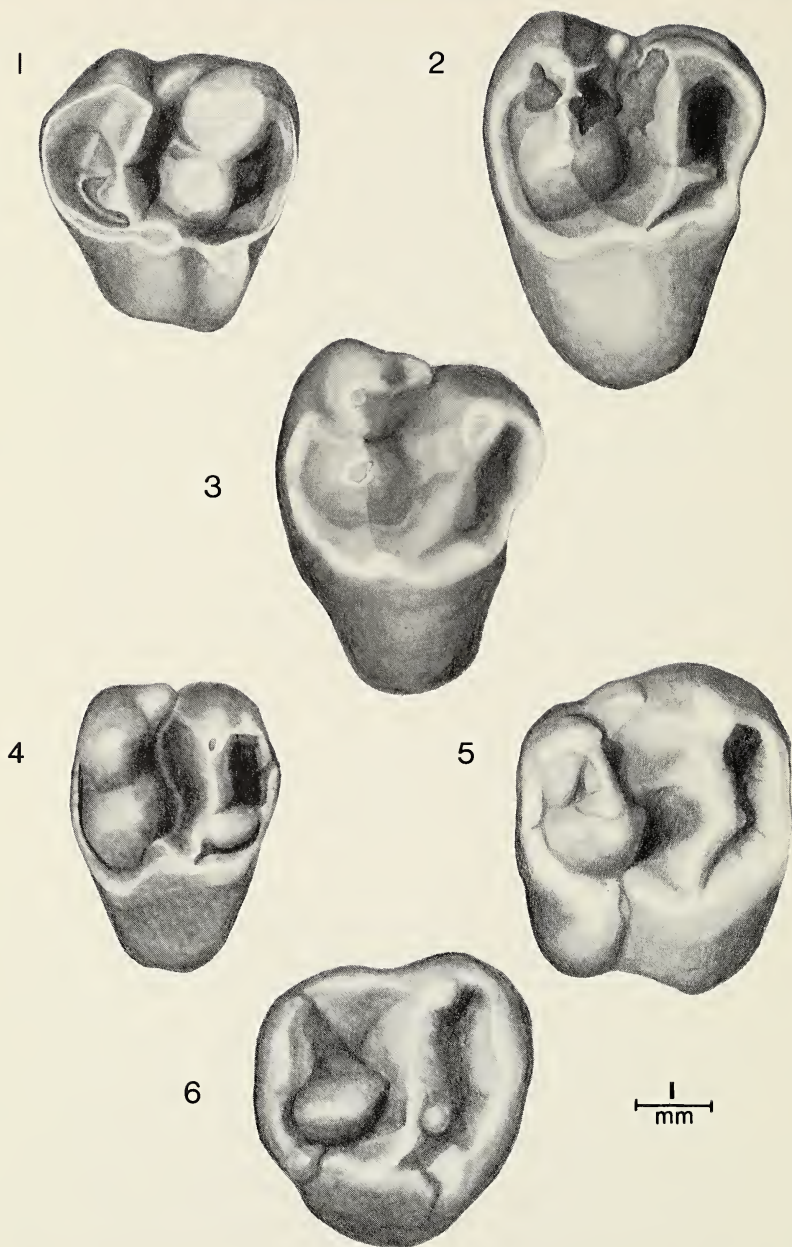
<sup>1</sup>Named for John E. Guilday in appreciation of his valued advice and criticism.

any of the  $P^4$ s, as the metaconules simply merge into the base of the protocone. Protolophs are somewhat more distinct, and small protoconules are present. Each  $P^4$  has a small mesostyle.

There are two somewhat different types of teeth grouped here as  $M^1$  or 2. One type (fig. 4) consists of molars that are slightly wider in relation to their length than are the others. Also, these teeth have a less prominent hypocone with little or no grooving of the internal face. The squarer teeth of the second type (fig. 5) have large hypocones distinctly set off from the protocones by an internal groove. These two types may represent first upper molars (group 1) and second upper molars (group 2). In other characters the teeth are all similar. Each has a large metaconule, usually set off from the protocone, complete protoloph, but no metaloph. In some cases (fig. 4) a protoconule is present, but generally it is absent. The size and position of the mesostyle is variable.

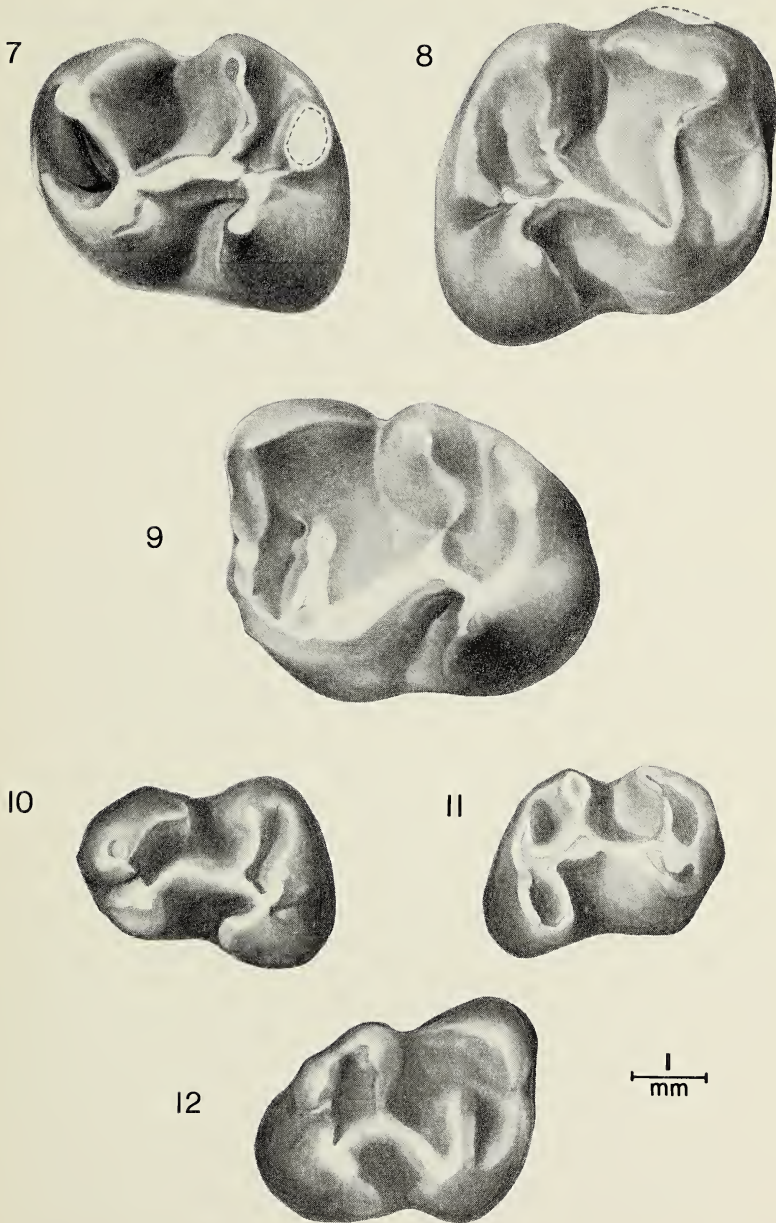
There is one  $M^3$  from the Rodent locality, and three from the Wood locality. All teeth are circular in occlusal outline. All three teeth from the Wood locality have a distinct protoconule set just anterior to the protoloph and not incorporated within it. This cusp is absent in the one specimen from the Rodent locality. In other respects the teeth are similar. There is no hypocone and little, if any, indication of a metacone. Rather, the entire posterior loph from protocone around through the postero-external corner is swollen, especially in the region of the metacone. There is a large, partially isolated metaconule present on all specimens. On one specimen (CM 19774) there is a short crest from the metaconule to the protoloph.

There is considerable variation in the lower fourth premolars, particularly in the size of the protoconid and development of the anterior cingulum. There are three  $P_4$ s from the Rodent locality and three from the Wood locality. In CM 14626 the protoconid is not at all prominent, whereas in CM 15342 and 18231 it is distinct. In the other premolars the protoconid is moderately developed. In CM 14626 there is a strong but short anterior cingulum that passes from the small protoconid into the anterior slope of the metaconid. The anterior cingulum is absent on CM 15340, 18231, and UCM 24793, but is present as a very narrow shelf at the base of the anterior face of CM 15342. On all premolars the ectolophid and hypolophid are strong and the buccal valley is broad. The hypolophid passes directly across the occlusal surface from entoconid to ectolophid. There are no metastylids or mesoconids present. The hypoconulids are distinct on all premolars, and the posterior cingula merge



Figs. 1-6. *Leptotomus guildayi*. 1. CM 16065, LdP<sup>4</sup>. 2. CM 14621, RP<sup>4</sup>. 3. CM 15353, RP<sup>4</sup>. 4. CM 21980, LM<sup>1-2</sup>. 5. CM 15350, RM<sup>1-2</sup>. 6. CM 15346, RM<sup>3</sup>.





Figs. 7-12. *Leptotomus guildayi*. 7. CM 14626, LP<sub>4</sub>. 8. CM 14628, RM<sub>1,2</sub>. 9. CM 14627, LM<sub>3</sub>, Type. 10. CM 18231, LP<sub>4</sub>. 11. CM 15340, RM<sub>1,2</sub>. 12. CM 10014, RM<sub>3</sub>.



into the posterior slopes of the entoconids near their base. One or more of these teeth, particularly CM 15342, may be a deciduous premolar, but it is impossible to be certain of this in the absence of roots on the teeth.

There is very little variation in the occlusal pattern of the ten first and second lower molars here assigned to *Leptotomus guildayi*. They all display large trigonid basins with complete metalophids posteriorly and strong anterior cingula anteriorly. The anterior cingula lie well below the tip of the protoconids and generally somewhat below the level of the metalophids. The trigonid basins enclosed between these two lophs are shallow but wide. The buccal valleys of the first and second molars are wide, and swing slightly posteriorly behind the hypoconids. The ectolophs are long, heavy crests on all teeth. The hypoconulids are always large and are distinctly set off from the hypoconids by a constriction in the posterior loph. This loph, or posterior cingulum, then either passes from the hypoconulid into the base of the entoconid (CM 14628; fig. 8), or ends before reaching the entoconid, leaving a postero-internal opening into the posterior valley (CM 16770). Hypolophids are strong on all specimens, passing almost directly across the crown towards the ectolophid and curving sharply anteriorly just as they merge with the ectolophid.

There are six  $M_3$ s, four from the Rodent locality and two from the Wood locality. As with the first and second molars, there is very little variation in occlusal pattern. The third molars are, in fact, quite similar to  $M_1$  and  $M_2$ , differing only in the enlargement of the hypoconid, hypoconulid, and the valley between the hypolophid and posterior crest. The entoconid is isolated as a prominent cusp, with a notch between it and the hypoconulid. The hypolophid is strong and runs directly across the crown to the ectolophid. As in the other molars, the trigonid basins are wide but shallow, with well-developed anterior cingula and metalophids. The buccal valleys are wide, and curve slightly behind the hypoconid. Wood (1949a, p. 557) referred a single cheek tooth, an  $M_3$ , to ?*Rapamys* sp. Two of the above  $M_3$ s come from the exact locality at which Wood's specimen was found. They match Wood's specimen completely (figs. 9 and 12), as do the other specimens referred here to *Leptotomus guildayi* from the Rodent locality just to the east.

MEASUREMENTS IN MM., *Leptotomus guildayi*

		N	M	OR	M <sub>R</sub> (N)	M <sub>W</sub> (N)
dP <sup>4</sup>	a-p	1	3.44	...	...	...
	tr	1	3.68	...	...	...
P <sup>4</sup>	a-p	4	3.76	3.50-4.00	3.88(2)	3.60(2)
	tr	4	4.75	4.30-4.95	4.96(2)	4.56(2)
M <sup>1</sup> or <sup>2</sup>						
	a-p	10	3.85	3.50-4.15	4.05(3)	3.80(7)
	tr	10	4.75	4.00-5.30	5.00(3)	4.65(7)
M <sup>3</sup>	a-p	3	3.97	3.75-4.00	4.00(1)	3.96(2)
	tr	3	3.84	3.70-4.00	3.84(1)	3.84(2)
P <sup>4</sup>	a-p	6	4.26	4.00-4.50	4.27(3)	4.24(3)
	tr	4	2.96	2.80-3.05	3.00(2)	2.92(2)
	tr	5	3.62	3.35-4.00	3.68(2)	3.60(3)
M <sub>1</sub> or <sub>2</sub>						
	a-p	10	4.22	4.00-4.50	4.30(3)	4.20(7)
	tr	10	3.58	3.20-3.85	3.75(3)	3.50(7)
	tr	9	3.90	3.50-4.15	4.00(3)	3.90(6)
M <sub>3</sub>	a-p	6	4.65	4.50-4.95	4.63(4)	4.60(2)
	tr	6	3.92	3.85-4.00	3.92(4)	3.92(2)
	tr	6	3.60	3.45-3.75	3.59(4)	3.68(2)

**AFFINITIES:** It is extremely difficult to justify assignment of this species to any of the ischyromyid genera as diagnosed by Wood (1962), yet there are no characters that, in my opinion, warrant recognition of a new genus for this material. The dentition is in general rather simple, as in *Leptotomus* and *Ischyrotomus*, in contrast with the more complex dentitions of *Mytonomys* and *Rapamys*. *Tapomys*, also known from the late Eocene, appears to be referable to *Leptotomus* as discussed in a following section.

*Leptotomus guildayi* is placed in *Leptotomus* primarily because of the lack of specializations in the upper and lower molars. In *Leptotomus*, as defined by Wood (1962:64, 68), the cusps are high; there is little or no crenulation in the dentition; a ridge develops, in some later species, from the entoconid toward the hypoconid; the protoconid of P<sub>4</sub> seems to be displaced into and behind the metaconid; hypocones are progressively developed on M<sup>1</sup> and M<sup>2</sup>; and there are no accessory conules in the upper molar lophs. These characters are all to be found to some degree in *Leptotomus guildayi*. *Leptotomus* is also characterized, however (*op. cit.*), as having reduced basins, a tendency for migration of the anterior cingulum around onto the buccal side of the paracone on P<sup>4</sup>-M<sup>3</sup>, and well-developed mesoconids on the ectolophids of M<sub>1</sub>-M<sub>3</sub>. These characters are not found in *Leptotomus guildayi*.

Additionally, this Badwater species is distinct in having a low but complete loph extending from the entoconid to the posterior end of the

ectolophid, in having very large and enclosed trigonid basins, and in having wide buccal valleys on  $M_1$ - $M_3$ . The upper dentition does not show any particular specializations, and there is no indication of buccal migration of the anterior cingulum.

The dentition of *Mytonomys* (Wood, 1962, fig. 84; Black, 1968b) is much too complex to bear any close relationship to that of *Leptotomus guildayi*. This is also true for the dentition of *Rapamys* (Wood, 1962, fig. 52; figs. 25-40, this paper). In addition, the hypolophid is a much more complete crest in *Leptotomus guildayi* than in either *Mytonomys* or *Rapamys*. Wood (1949a; 1962) referred an isolated  $M_3$ , part of an  $M_1$  or 2, and an incisor from Badwater (from the Wood locality) to *Rapamys* sp. In 1949, he stated that more material might show that a distinct genus should be recognized for this species. Reason for reference of the Badwater specimen to *Rapamys* hinged on the separation of entoconid and posterolophid, and presence of a hypolophid in both forms. Now that the complete dentition of the Badwater form is known, reference of this species to *Rapamys* does not appear possible. A species of *Rapamys* is present at some of the Badwater localities, but it was not represented in Wood's 1948 collection.

It seems best, therefore, to consider the present sample as belonging to a species of *Leptotomus* possibly derived from *Leptotomus bridgerensis*. The incipient development of a hypolophid seen in some other species of *Leptotomus* was carried much further in *Leptotomus guildayi*, as was the strengthening of the metalophid and enlargement of the trigonid basin. In *L. bridgerensis*, the metalophid is complete on  $M_1$ - $M_3$ , but the trigonid basin is not enlarged. This is essentially the condition in *Leptotomus tapensis*, although that species is larger than *L. bridgerensis*. *L. tapensis* thus differs from *L. guildayi* in having a smaller trigonid basin and much less development of the hypolophids. While these changes were taking place in the lower dentition, the upper cheek teeth of *L. guildayi* changed little from those of *L. bridgerensis*. There was only a slight increase in size from *L. bridgerensis* to *L. guildayi*. The populations from localities 5 and 6 described below would seem to be intermediate between *Leptotomus bridgerensis* and *L. guildayi*.

It does not now appear likely that *Leptotomus guildayi* gave rise to any later ischyromyids. Earlier (Black, 1968a:299) I had thought that this material might be referable to *Rapamys* and that this species might have been ancestral to *Ischyromys*. I no longer believe this to be so, however, as some specimens of ?*Ischyromys* contemporaneous with *Lepto-*



*tomus guildayi* are present at the Wood locality. Also, I now restrict *Rapamys* to those forms having complex upper dentitions with doubled metacones or metaconules with accessory lophs or both. This type of dentition is not at all what one would expect in the ancestry of *Ischyromys*. In 1967 (Black, 1968a) I had not recognized in the Badwater collection the *Rapamys* population described below, but was following Wood (1962) in his identification of ?*Rapamys* sp. from Badwater. His material is certainly referable to *Leptotomus guildayi* and does not pertain to *Rapamys*.

*Leptotomus* near *L. guildayi*

Figures 13-24

MATERIAL: CM 16875, LP<sup>4</sup>-M<sup>1</sup>; CM 14569, RM<sup>1</sup>-M<sup>2</sup>; CM 16873, LP<sub>4</sub>-M<sub>2</sub>; dP<sup>4</sup>, CM 16869, 16874, 16877; P<sup>4</sup>, UCM 24741, 24764; M<sup>1</sup> or <sup>2</sup>, CM 14510, 15320, 15325, 15563, 16876, 19746, 25352; M<sup>3</sup>, CM 15575; dP<sub>4</sub>, CM 16868; P<sub>4</sub>, CM 16791, 16870, UCM 24799; M<sub>1</sub> or <sub>2</sub>, CM 14508, 14568, 15331, 15337, 15576, 16872, 16880, 16885, 19764, UCM 24728, 24744, 24789; M<sub>3</sub>, 14507, 15330, 15417, 16794, 16871.

DISTRIBUTION: Localities 5, 5A, and 6.

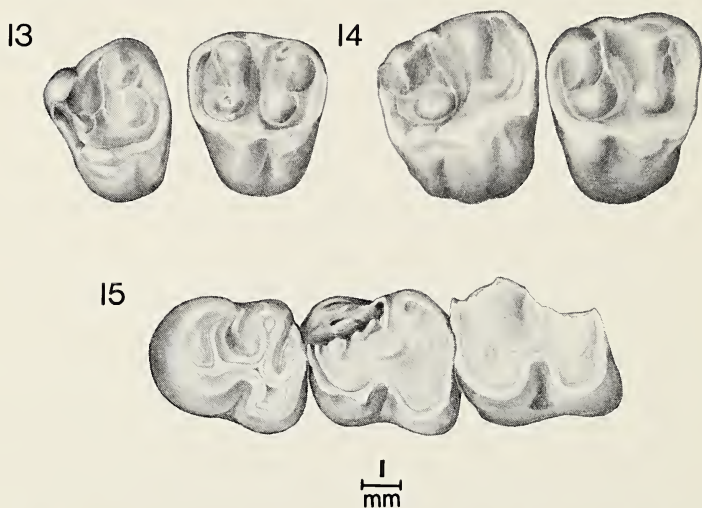
DESCRIPTION: The deciduous fourth upper premolars are all triangular in occlusal outline. The protocone is a high, rather sharp antero-posteriorly compressed cusp, and there is little or no indication of a hypocone posterior to it. The anterior cingulum is broad, but there is no parastyle. The paracone, protocone, metacone, and metaconule are all distinct cusps that rise well above the rest of the surface of the tooth. A small protoconule is discernible within the protoloph, but it is neither as large nor as distinctly isolated as the metaconule. There is a very low loph from the protoconule to the anterior cingulum dividing the anterior shelf into two parts. Posteriorly, the posterior cingulum curves around the outside of the metacone and onto the buccal face of the tooth.

The two upper permanent P<sup>4</sup>s from locality 5 differ somewhat from the one P<sup>4</sup> known from locality 6. Those from locality 5 are somewhat larger and more triangular in occlusal outline than the single tooth from locality 6. This difference in occlusal outline is due primarily to the anterior and somewhat internal position of the paracone on the specimen from locality 6 (CM 16875). In all other morphological details these teeth are quite similar. The protocone is the only internal cusp and it is situated anteriorly more or less directly internal to the paracone. The metaloph diverges from the protocone postero-buccally to reach the metacone, and the protoloph passes almost directly from the protocone buccally to the paracone. There is a small protoconule, but a large, separate metaconule. The metaconule in all instances is equal in size to



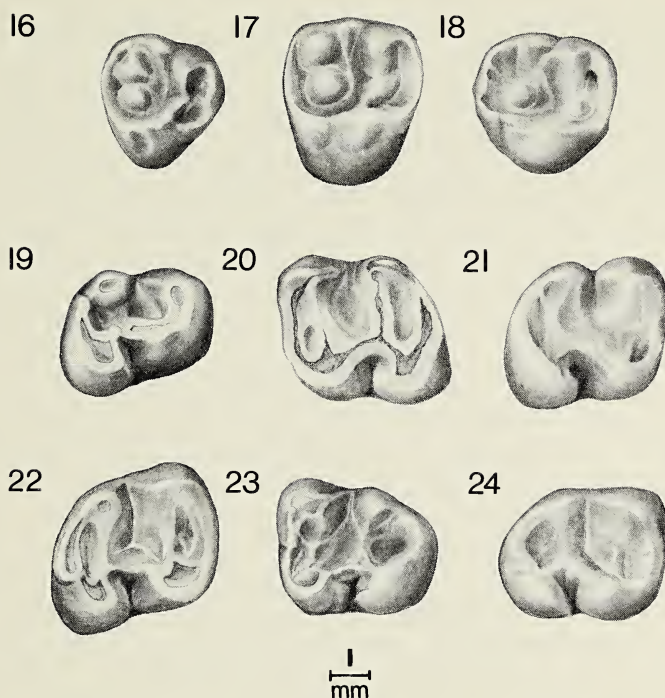
the metacone. The anterior cingulum is short and narrow. There is no mesostyle on any of the  $P^4$ s.

There is one maxillary fragment that preserves  $M^1$ - $M^2$  (CM 14569) and one maxillary fragment (CM 16875) with  $P^4$ - $M^1$ . Otherwise, all the upper first and second molars are isolated teeth. On these teeth, the hypocone is generally large and is separated from the protocone by a distinct groove down the internal face of each tooth. The anterior cingula are wide but low, and do not rise into prominent parastylar areas anterior to the paracones. The protoloph is generally complete, with a thin, low ridge connecting the protoconule to the face of the protocone. In contrast, the metalophs are incomplete, ending in an enlarged metaconule which is distinctly separated from the hypocone. Mesostyles are generally present, although small. The posterior cingula are narrow and short, failing to reach the buccal margins of the teeth. The upper first and second molars from locality 5 are somewhat larger than those from locality 6, but in details of morphology, the two samples agree closely.



Figs. 13-15. *Leptotomus* near *L. guildayi*. 13. CM 16875,  $LP^4$ - $M^1$ . 14. CM 14569,  $RM^1$ - $M^2$ . 15. CM 16873,  $LP_4$ - $M_2$ .

Only one  $M^3$  in the collection is believed to represent this species. This tooth is circular in occlusal outline, with a very broad protocone. The protoloph is very low and there is a distinct protoconule abutting against the internal face of the protocone. The metaconule is distinct and is isolated in the talonid basin. The posterior half of  $M^3$  is ringed by a



Figs. 16-24. *Leptotomus* near *L. guildayi*. 16. CM 16877, RdP<sup>4</sup>. 17. CM 19746, RM<sup>1-2</sup>. 18. CM 15575, RM<sup>3</sup>. 19. CM 16870, RP<sup>4</sup>. 20. CM 16885, LM<sup>1-2</sup>. 21. CM 19764, RM<sup>1-2</sup>. 22. CM 15337, RM<sup>1-2</sup>. 23. CM 15417, LM<sup>3</sup>. 24. CM 16794, RM<sup>3</sup>.

thin, curving loph, which passes from the posterior slope of the protocone around and into the base of the paracone. There is no distinct swelling of this ridge in the area of the metacone.

The deciduous fourth lower premolar is somewhat smaller than the permanent P<sub>4</sub>. It also differs from the permanent teeth in having a distinct protoconid with a small notch between the protoconid and metaconid. In addition, the hypolophid is a complete crest on the deciduous P<sub>4</sub>, but not on the permanent teeth.

The permanent fourth lower premolars show no indication of a separate protoconid. The metaconid is an extremely high, very massive cusp, occupying the entire anterior margin of the teeth. There is no notch on the anterior face of these teeth, and no sign of a trigonid basin. The hypoconid and entoconid, although bulbous, lie considerably below the top of the metaconid. There is a low, short ridge from the entoconid into the talonid basin, but it does not reach the ectolophid.

The first and second lower molars are rectangular in occlusal outline, being somewhat longer than they are wide. The metaconid is the largest cusp on  $M_1$ - $M_2$  and projects well above the tops of the entoconid, hypoconid, and protoconid. The trigonid basin on  $M_1$  and  $M_2$  is relatively small and generally closed posteriorly by the metalophid, which is quite heavy. There is no mesostylid or mesoconid. The ectolophid is low and rather weak. Internally there is a deep notch between the entoconid and the posterior slope of the metaconid, leaving the talonid basin open lingually. The posterolophid between the hypoconid and the entoconid is elevated into a rather heavy crest, with no notch between the posterolophid and the entoconid. Development of the hypolophid from entoconid to the ectolophid is variable, but in no specimen is it a high, strong crest. In most cases, the hypolophid is very low, but does pass buccally to fuse with the ectolophid. There is no distinct hypoconulid on any of the first or second lower molars.

The third lower molar is the largest of the lower cheek teeth, and resembles  $M_1$ - $M_2$  in general pattern. It differs from the first and second molars in having a more expanded posterior portion of the tooth with a heavy, swollen posterolophid curving from the hypoconid into the entoconid. The hypolophid on  $M_3$  is low but complete, passing from near the base of the entoconid to the ectolophid. The trigonid basin is variable in size, being relatively large on one specimen (CM 16794) but small on another (CM 15417).

The incisor (CM 16873) is compressed laterally and is very deep antero-posteriorly. The enamel is thin and covers about half the lateral face of the incisor, overlapping just slightly on to the medial face. The portion of the mandible that is preserved is deep below the cheek teeth. There are two mental foramina, a small one lying just below the middle of  $M_1$  and a larger one lying forward at about the middle of the diastema and just below the superior diastema surface.

MEASUREMENTS IN MM., *Leptotomus* NEAR *L. guildayi*

		N	M	OR	$M_5(N)$	$M_6(N)$
dP <sup>4</sup>	a-p	3	...	2.80-3.20	...	3.03(3)
	tr	3	...	3.10-3.50	...	3.37(3)
P <sup>4</sup>	a-p	3	3.13	3.00-3.20	3.20(2)	3.00(1)
	tr	3	4.20	4.10-4.30	4.25(2)	4.10(1)
M <sup>1</sup> or <sup>2</sup>	a-p	10	3.67	3.40-4.10	3.72(7)	3.53(3)
	tr	10	4.47	4.10-4.90	4.59(7)	4.20(3)
M <sup>3</sup>	a-p	1	3.70	...	...	...
	tr	1	3.70	...	...	...



(MEASUREMENTS, *Leptotomus* NEAR *L. guildayi*, CONTINUED)

		N	M	OR	M <sub>5</sub> (N)	M <sub>6</sub> (N)
dP <sub>4</sub>	a-p	1	3.10	...	...	...
	tr	1	2.00	...	...	...
	tr	1	2.60	...	...	...
P <sub>4</sub>	a-p	3	3.56	3.50-3.70	3.50(2)	3.70(1)
	tr	3	2.50	2.30-2.80	2.35(2)	2.80(1)
	tr	3	2.97	2.80-3.20	2.85(2)	3.20(1)
M <sub>1</sub> or <sub>2</sub>	a-p	12	3.85	3.50-4.20	3.84(9)	3.87(3)
	tr	11	3.48	2.90-4.00	3.54(8)	3.33(3)
	tr	10	3.52	3.10-4.00	3.48(8)	3.70(2)
M <sub>3</sub>	a-p	5	4.18	3.90-4.40	4.15(4)	4.30(1)
	tr	5	3.51	3.10-3.90	3.40(4)	3.90(1)
	tr	5	3.30	3.00-3.50	3.25(4)	3.50(1)

AFFINITIES: *Leptotomus* near *L. guildayi* is somewhat smaller than *Leptotomus guildayi* from the Wood and Rodent localities. These specimens from localities 5 and 6 also differ from those of *Leptotomus guildayi* in having a weaker hypolophid on M<sub>1</sub>-M<sub>2</sub> and in having somewhat smaller but deeper trigonid basins on the lower molars. The pattern of the upper cheek teeth is quite similar for samples from all four localities. In all, there does not seem to be enough difference between the populations found at localities 5 and 6 and those from the Wood and Rodent localities to warrant specific separation of the two groups. On present evidence, the population found at localities 5 and 6 was probably ancestral to *Leptotomus guildayi* of the Wood and Rodent localities.

*Leptotomus* near *L. guildayi* is closer, morphologically, to *L. tapensis* than is *L. guildayi*, particularly in possessing the lower, less robust hypolophid and in having a smaller trigonid basin. *Leptotomus* near *L. guildayi* is considerably smaller than *L. tapensis*, however.

**Rapamys wilsoni<sup>1</sup>, new species****Figures 25-38**

TYPE: CM 15564 RM<sup>1</sup> or <sup>2</sup>.

HYPODIGM: Type and P<sup>4</sup>, CM 14786, 15420, 15422, UCM 24785; M<sup>1</sup> or <sup>2</sup>, CM 14502, 15322, 15328, 15561, 15564, UCM 24798; M<sup>3</sup>, CM 14787, UCM 24723; dP<sub>4</sub>, 15324; P<sub>4</sub>, CM 14503, 15326, 15569, 15573, 15574, 16884, UCM 24729, 24771; M<sub>1</sub> or <sub>2</sub>, CM 15327, 15329, 15418, 15581, 19763, UCM 24747, 24820; M<sub>3</sub>, CM 15332, 16879.

DISTRIBUTION: Type from Locality 5. All other specimens from 5 and 5A except CM 15581, 16878, and 16884, which are from Locality 6.

<sup>1</sup>Named for R. W. Wilson, for his work on late Eocene rodents of California.



DIAGNOSIS: Smaller than *Rapamys fricki*; metacone single, smaller than doubled metaconule on M<sup>1-2</sup>; valley between paracone and metacone open buccally; protocone and hypocone not as deeply separated as in *R. fricki*; lower molars not as elongate as in *R. fricki*; trigonid basins larger and hypolophids somewhat stronger than in *R. fricki*.

DESCRIPTION: The fourth upper premolars are triangular in occlusal outline. The protocone is the main central internal cusp. On one specimen, CM 14786, there is no distinct hypocone. The other specimens have distinct hypocones, although they are considerably smaller than the protocones. The protoloph is weakly developed and the metaloph is incomplete. The paracone is considerably larger than the protoconule, but in the posterior half of the tooth the metaconule is considerably larger than the metacone. On one premolar there is a very small mesostyle, but this cusp is absent on the other premolars. The anterior cingulum is rather narrow and does not rise to a high parastylar ridge at the antero-buccal corner of the teeth.

The first and second upper molars are squarer in occlusal outline than the premolars. This is due primarily to the enlargement of the hypocone. The groove between the hypocone and the protocone along the internal face of the upper molars is not as deep as it is in *Rapamys fricki*, but it is distinct and separates the two cusps. The protoloph on the upper molars is generally well developed and joins the protocone at its antero-internal corner. Between the protoloph and the metaconule, there is a heavy ridge passing from the top of the protocone into the central valley between the protoconule and the metaconule. The metaloph on all first and second molars does not reach the hypocone. In some teeth, it is also interrupted between the metacone and the metaconule, and on others there is a crest between these two cusps. The metaconule is always larger than the metacone, and is generally partially divided into a smaller, anterior cusp and the larger interior portion of the cusp. There is considerable variation in the upper molars in development of the mesostyle. In some cases, e.g. UCM 24798, the mesostyle is barely distinct, while in others it is either a distinct cusp (CM 15322) or is elongated into a ridge passing internally towards the protocone, as in CM 15564. In all cases, however, the central valley between the paracone and the metacone is open internally, with no indication of the posterior paracone buttress seen in *Rapamys fricki*.

The third upper molars are circular in occlusal outline, with no indication of a distinct hypocone. The protoloph is always complete, with the protoconule either completely submerged within the loph or developed



Figs. 25-38. *Rapamys wilsoni*. 25. CM 15420, RP<sup>4</sup>. 26. UCM 24785, LP<sup>4</sup>. 27. CM 14786, LP<sup>4</sup>. 28. UCM 24798, RM<sup>1-2</sup>. 29. CM 15564, RM<sup>1-2</sup>, Type. 30. CM 15322, LM<sup>1-2</sup>. 31. CM 14787, RM<sup>3</sup>. 32. UCM 24723, LM<sup>3</sup>. 33. CM 15234, LdP<sup>4</sup>. 34. UCM 24771, RP<sup>4</sup>. 35. CM 15581, RM<sup>1-2</sup>. 36. CM 19763, RM<sup>1-2</sup>. 37. CM 15329, LM<sup>1-2</sup>. 38. CM 16879, LM<sup>3</sup>.

as a very distinct large cusp, as it is in UCM 24723. On the third upper molars there is a heavy ridge passing from the protocone between the protoloph and metaconule, as on the first and second upper molars. The metaconule is distinctly divided into two almost subequal cusps, and joins the ridge from the mesostyle. This ridge and the divided metaconules are distinctly set off from the postero-buccal corner of the tooth,

the metacone area. This area is expanded into a heavy, swollen, semi-circular ridge.

The fourth lower deciduous premolar is smaller and less robust, with smaller, more delicate cusps than the permanent P<sub>4</sub>. The metaconid is the largest cusp, with the protoconid, hypoconid, and entoconid of nearly equal size, all lying somewhat lower than the metaconid. The trigonid basin on the deciduous premolar is small, and opens both anteriorly and posteriorly. The hypolophid is also small, appearing to be merely a short ridge passing from the entoconid toward the hypoconid. The principal cusps on the permanent fourth lower premolar are all strong and rounded. The protoconid and metaconid are subequal and appressed to the trigonid basin, appearing as a very narrow slit between the two. The hypolophid is not well developed on the permanent premolar and fails to reach the ectolophid. The hypoconulid is well developed, and is almost the same size as the entoconid.

On the lower first and second molars, the trigonid basins are generally well developed and are closed both anteriorly and posteriorly by narrow crests. The four principal cusps are high and rather bulbous, and the hypoconulid is always strong. The extent of hypolophid development is variable. In some cases it is a complete loph from the entoconid to the ectolophid, whereas in others it just fails to join the ectolophid. The buccal valley on the lower molar is long, and curves posteriorly as it passes into the tooth. The hypoconid is swollen in all teeth, and is pulled anteriorly.

There is only one third lower molar in the collection. The trigonid basin of this tooth is small and is open posteriorly. The hypolophid is well developed, passing all the way across the tooth to the ectolophid. There is no indication of a mesostylid on any of the lower cheek teeth.

MEASUREMENTS IN MM., *Rapamys wilsoni*

		N	M	OR
P <sup>4</sup>	a-p	4	2.80	2.70-3.00
	tr	4	2.97	2.85-3.20
M <sup>1</sup> or <sup>2</sup>	a-p	6	3.31	3.20-3.70
	tr	6	3.95	3.75-4.35
M <sup>3</sup>	a-p	2	3.52	3.50-3.55
	tr	2	3.52	3.45-3.60
dP <sub>4</sub>	a-p	1	3.20	...
	tr	1	2.00	...
	tr	1	2.55	...



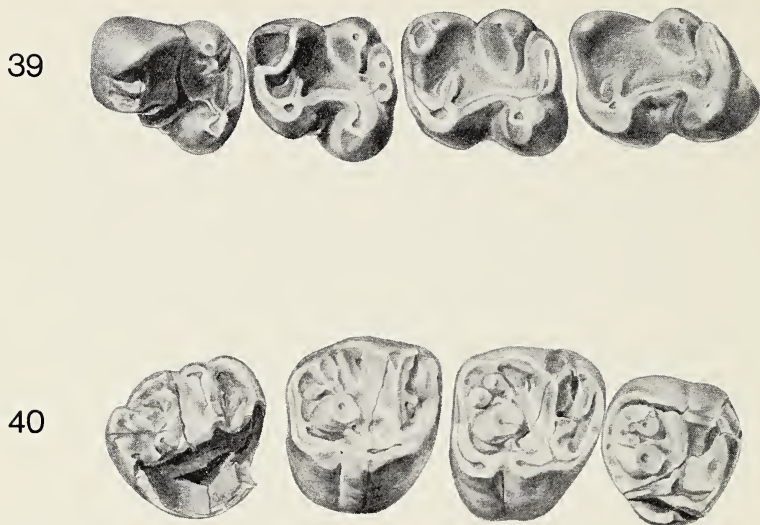
(MEASUREMENTS, *Rapamys wilsoni*, CONTINUED)

		N	M	OR
P <sub>4</sub>	a-p	6	2.97	2.70-3.20
	tr	6	1.98	1.75-2.20
	tr	6	2.51	2.35-2.55
M <sub>1</sub> or 2	a-p	7	3.60	3.25-3.95
	tr	7	2.75	2.35-2.55
	tr	7	3.30	3.10-3.75
M <sub>3</sub>	a-p	2	3.62	3.55-3.70
	tr	2	2.82	2.80-2.85
	tr	2	2.95	2.90-3.00

AFFINITIES: Specimens here assigned to a new species, *Rapamys wilsoni*, are all clearly distinct from any other Badwater ischyromyids, but do share a number of characters with *Rapamys fricki*, known from the late Eocene of California (Wilson, 1940). The major points of resemblance between these two species are found in the additional complications of the occlusal pattern of the upper cheek teeth, particularly in the doubling of the metaconules in *Rapamys wilsoni* and the metacones in *Rapamys fricki*. In addition, these two species are similar in having the hypocone and protocone separated in the upper molars; the distinct protoconules in the protoloph of M<sup>1</sup> and M<sup>2</sup>; the partial hypolophid development in the lower cheek teeth; and the distinct and large hypoconulid set off from the entoconid. The upper and lower dentition of *Rapamys fricki* is here refigured (figs. 39 and 40) to facilitate comparison with the Badwater specimens.

*Rapamys wilsoni* differs from *Rapamys fricki* in a number of minor details. These include the presence in *R. wilsoni* of a strong ridge from the protocone, which passes between the metaconule and the protoloph; the somewhat larger and more enclosed trigonid basins on the lower molars; and the slightly better-developed ridge from the entoconid towards the ectolophid on M<sub>1</sub>-M<sub>2</sub>. Perhaps the most striking difference between the two species lies in the doubling of a different cusp on the metaloph of M<sup>1</sup>-M<sup>2</sup>. In *Rapamys fricki* the outer or postero-external cusp is doubled. Wood (1962:150) considers this doubled cusp to be the metaconule, whereas Wilson (1940:75) interpreted the doubled cusp as the metacone. Wilson's interpretation is followed here. Thus in *Rapamys fricki*, the metacone is doubled, whereas in *Rapamys wilsoni* it is the internal cusp on the metaloph, the metaconule, that is doubled. The same function, increasing the rugosity or amount of wear surface along the metaloph, is performed in both instances, and I do not believe the dif-





Figs. 39-40. *Rapamys fricki*. 39. LACM (CIT) 2181, LP<sub>4</sub>-M<sub>3</sub>, Type. 40. LACM (CIT) 2183, RP<sub>4</sub>-M<sub>3</sub>.

ference in locus of splitting a single cusp into two parts to be of more than specific importance.

Wood (1962:152-153) considered two other species as possibly belonging in the genus *Rapamys*. These were *Rapamys* sp. A., represented by two teeth earlier referred by Wilson (1940) to *Leptotomus burkei* (an incisor) and *Leptotomus* near *burkei* (an upper molar), and ?*Rapamys* sp. B., based on fragmentary material from Badwater, Wyoming. I have here assigned this Badwater material to *Leptotomus guildayi*. *Leptotomus burkei* (Wilson, 1940:73) is now considered to be a species of *Mytonomys* (Wood, 1956; Black, 1968b). The upper molar [LACM (CIT) 2178] referred by Wilson (1940) to *Leptotomus* near *burkei* and figured by Wood (1962, fig. 52 I as pertaining to *Rapamys* sp. A.), is similar to the upper molars here assigned to *Leptotomus guildayi* and is probably referable to the genus *Leptotomus*. On the basis of size and general morphology, the single tooth [LACM (CIT) 2178] from locality 207 of the Simi Valley, Ventura County, California, might well be an isolated upper molar of the species *Ischyrotomus* (?) *tapensis* Wilson (1940:69). This species was later referred to a new genus, *Tapomys*,

by Wood (1962). In erecting the new genus Wood (1962:154) said, "the cheek teeth of this genus are very similar to those of some of the more primitive species of *Paramys* and even closer in pattern to *Leptotomus*." In the succeeding discussion (Wood, 1962:154-157) of *Tapomys tapensis*, similarities to or differences from *Leptotomus* are not referred to again. The dentition of *Leptotomus* is slightly more complex than that of *Ischyrotomus* in showing trends toward hypolophid development and some accessory crenulation of enamel. In addition, the lower molars of *Leptotomus* are longer than they are wide and not as massive as those of *Ischyrotomus*. In both genera the dentition is much less specialized than in contemporaneous species of *Rapamys*, *Mytonomys*, and *Thisbemys*. The presence of slight crenulations of the enamel, the incipient entoconid cresting, and the elongate lower molars of the cheek teeth of *Tapomys tapensis* are all characters that are also found in species of *Leptotomus*. For this reason it seems likely that the material on which *Tapomys tapensis* is based is indistinguishable, on a generic level, from *Leptotomus*.

To summarize this rather confusing array of species:

*Ischyrotomus* (?) *tapensis* Wilson, 1940:69

= *Tapomys tapensis* Wood, 1962, p. 154.

= *Leptotomus tapensis*, this paper.

LACM (CIT) 2178 M<sup>1</sup> or <sup>2</sup>, *Leptotomus* near *L. burkei* Wilson, 1940:75

= *Rapamys* sp. A. Wood, 1962:153.

= *Leptotomus tapensis*, this paper.

Elsewhere in this paper ischyromyids of the California late Eocene are compared in detail with the Badwater assemblage.

Wood (1962:152) discussed the possible relationship of *Rapamys* to the ancestry of the caviomorph rodents of South America. The rodent immigrant into South America from whom the later South American rodents were evolved was probably a member of the Ischyromyidae. On the basis of all available material of this family, there is little reason to suggest that one genus was any more likely to be ancestral to the South American caviomorphs than any other.

Wood (*op. cit.*:152) says, "Certainly no known member of *Rapamys* is ancestral to the South American Caviomorpha, but its dentition unquestionably represents a structural intermediate between that of *Reithroparamys* and that of *Platypittamys*." The dentition of *R. fricki* is much too specialized in the development of accessory small lophs and the presence of doubled cusps in the upper molars to have been ancestral to *Platypittamys* (Wood, 1949b, fig. 3), in which the upper molar pattern

consists of four complete and uncomplicated transverse lophs. In *Rapamys* the trend is toward break-up of transverse lophs into small separate units. It is much easier to derive the general caviomorph ancestral condition from a less highly specialized ischyromyid like *Leptotomus* or *Paramys*.

The fact that the earliest known South American rodents are diverse (Wood & Patterson, 1959, fig. 34; Hoffstetter and Lavocat, 1970), and in their dental pattern clearly specialized beyond the North American ischyromyids suggests a period of occupancy in South America prior to the early Oligocene. Wood and Patterson (1959:396-401) argue convincingly that this colonization probably did not occur before mid-Eocene time. They prefer a late Eocene arrival for the colonizing stock from North America. There are several middle-to-late Eocene lineages of rather generalized ischyromyids known in North America (Wood, 1962, fig. 90), any one of which could be morphologically close to the ancestry of the Caviomorpha. Recently Hoffstetter and Lavocat (1970) described some new rodents from the early Oligocene of Bolivia, noting a number of resemblances of these genera to African phiomorphs. On present evidence it is impossible to be certain of the ancestry of the caviomorphs.

*Ischyrotomus* cf. *I. eugenei*

MATERIAL: CM 14567, partial left lower I, and 15338, partial right lower I.

LOCALITY: Locality No. 5.

DESCRIPTION: These two incisor fragments match perfectly the description given by Wood (1962:219, fig. 79E) for the lower incisors of *Ischyrotomus eugenei*. As Wood pointed out, the enamel on these incisors is extremely thin. The anterior tip of the incisor is preserved on CM 15338, but not on any of the *I. eugenei* material from Utah. The tip displays a very long wear-face with a distinctly stepped posterior border. Although no cheek teeth referable to *Ischyrotomus* have been found at any of the Badwater late Eocene localities, there can be little doubt that these two incisors should be referred to *I. eugenei*. They are much too large to belong to any other described ischyromyid, and they agree nearly perfectly in pattern with *I. eugenei*.

MEASUREMENTS IN MM.

CM 14567	left lower I	7.60 a-p	6.60 tr
CM 15338	right lower I	7.50 a-p	6.65 tr



*?Ischyromys* sp.

Figures 41-45

MATERIAL: CM 15385, LP<sup>4</sup>; 16020, LM<sup>1</sup> or <sup>2</sup>; 15354, RM<sup>1</sup> or <sup>2</sup>; 16016, LM<sup>3</sup>; 15348, LM<sub>1</sub> or <sup>2</sup>.

LOCALITY: Wood Locality.

DESCRIPTION: The upper fourth premolar can be separated from the molars, as it displays a more bulbous and more anteriorly projecting parastylar region and has a less obvious separation of the protocone and hypocone. On the molars the protocone and hypocone are set apart by a distinct cleft which passes most of the way down the lingual face of the teeth. On both P<sup>4</sup> and M<sup>1</sup>-M<sup>2</sup> the protoloph is complete, with no discernible protoconule, and the metaloph is interrupted and set off from the hypocone, terminating in a large metaconule. There is a small mesostyle on P<sup>4</sup> and on one of the two molars. The lophs are high, and the teeth display a marked unilateral hypsodonty. The M<sup>3</sup> is subcircular in occlusal outline, with an enlarged protocone and very heavy posterior border. This postero-internal region of the tooth is divided into three heavy ridges by narrow notches, which break up the heavy crest. There is a distinct metacone and metaloph, but no metaconule. The anterior cingulum is narrow and does not reach the buccal border of M<sup>3</sup>.

There is only a slight unilateral hypsodonty in the lower molar. The lophs are elevated, however, and separated by rather deep valleys. The trigonid basin is large and closed posteriorly. The hypolophid is prominent and passes to the ectolophid. The posterior cingulum is broad, but does not close off the posterior valley lingually. All major cusps stand above the level of the connecting lophs.

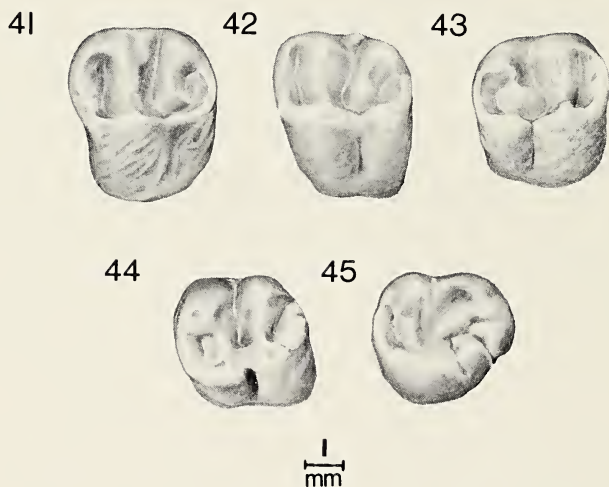
MEASUREMENTS IN MM., *?Ischyromys* sp.

		a-p	tr	tr
CM 15348	LM <sub>1</sub> or <sup>2</sup>	3.35	3.35	3.40
CM 15354	RM <sup>1</sup> or <sup>2</sup>	3.40	3.90	...
CM 15385	LP <sup>4</sup>	3.60	4.30	...
CM 16020	LM <sup>1</sup> or <sup>2</sup>	3.40	3.85	...
CM 16016	LM <sup>3</sup>	3.55	3.25	...

DISCUSSION: The lower molar is similar to that of *Ischyromys douglassi* (Black, 1968a:286), particularly M<sub>1</sub> of CM 10967. However, there is no suggestion in *?Ischyromys* sp. of a small cusp or loph on the posterior side of the metalophid, a structure found occasionally in *I. douglassi*. Also, the lower molars of *I. douglassi* are more rectangular in occlusal outline than the single Badwater tooth. In the upper cheek teeth,



?*Ischyromys* sp. differs from *I. douglassi* in having the metaloph completely separated from the hypocone. In other respects the teeth are similar. There is not enough material of ?*Ischyromys* sp. available to understand the range of variation present in the population. From study based on the few teeth at hand, it appears that the genus *Ischyromys* can be carried back into the late Eocene, and that the Badwater species could well have given rise to the early Oligocene *I. douglassi*.



Figs. 41-45. ?*Ischyromys* sp. 41. CM 15835, LP<sup>4</sup>. 42. CM 16020, LM<sup>1-2</sup>. 43. CM 15354, RM<sup>1-2</sup>. 44. CM 15348, LM<sup>1-2</sup>. 45. CM 16016, LM<sub>3</sub>.

### Ischyromyid spp.

#### Figures 46-50

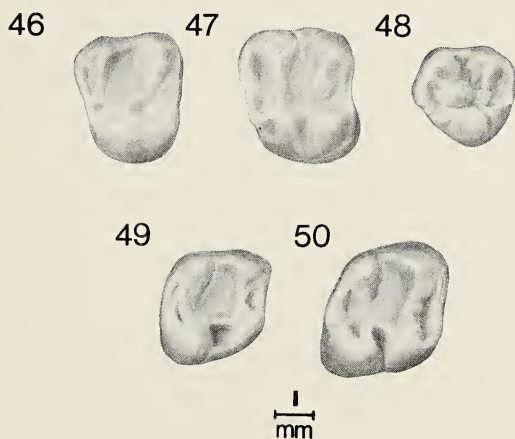
MATERIAL: LP<sup>4</sup>, CM 16014; M<sup>1</sup> or <sup>2</sup>, CM 15352, 18232; M<sup>3</sup>, CM 16084 (3 teeth); M<sub>1</sub> or <sub>2</sub>, CM 15345, 16073; M<sub>3</sub>, CM 15344.

DISTRIBUTION: All specimens are from the Wood locality except CM 18232, which is from the Rodent locality.

DESCRIPTION: The upper fourth premolar is distinct, with both the protoleph and the metaloph short and incomplete, failing to reach the base of the protocone. The paracone and metacone are widely separated, lying at the anterior and posterior external corners of the tooth. The central valley is therefore wide. Both the anterior and posterior cingula are narrow. There is no indication of a protoconule and there is only a faint swelling in the position of the metaconule. There is no distinct hypocone on this tooth. The mesostyle is absent.

The two upper first or second molars, one from the Rodent locality and one from the Wood locality, are identical in structure. There is a distinct hypocone on both teeth, which is set off from the protocone by a shallow, internal groove. The hypocone is somewhat smaller and set somewhat below the protocone. The protoloph is complete, with no indication of a protoconule. The metaloph fails to reach the protocone, and there is a slight swelling in the area of the metaconule. The central valley is rather narrow. There is no mesostyle at its buccal end.

The three third upper molars are all similar in morphology, although there is considerable variation in size. The teeth are circular in occlusal outline and they all show notching of the posterolophid, the anterior cingulum, and the protoloph. All these lophs are broken up into a series of cusps of various sizes. The protoloph is high and complete. There is a very large, distinct metaconule, buccal to the protocone, which is generally connected to the postero-external corner of the tooth.



Figs. 46-50. *Ischyromyid* spp. 46. CM 16014, LP<sup>4</sup>. 47. CM 18232, LM<sup>1-2</sup>. 48. CM 16084, LM<sup>3</sup>. 49. CM 16073, RM<sub>1-2</sub>. 50. CM 15345, RM<sub>1-2</sub>.

The two lower first or second molars are different from each other. One, CM 16073, is almost square in occlusal outline, whereas the other, CM 15345, is much wider than it is long. The latter tooth is in many ways reminiscent of the lower molars of some members of the *Sciuridae*. This tooth, CM 15345, has a rather long anterior cingulum set below the level

of the protocone, metalophid, and metacone. The cingulum and metalophid enclose a long, slit-like trigonid basin. The buccal valley is deep, but quite narrow antero-posteriorly. There is a small hypoconulid immediately posterior to the hypoconid. The posterolophid drops from the hypoconulid to the base of the entoconid. The entoconid is large and high, and there is no indication of a hypolophid from the entoconid into the talonid basin. There is a deep notch between the entoconid and the metaconid. The other tooth (CM 16073) has a very short anterior cingulum and a very small trigonid basin. The buccal valley is wide but not deep. There is no indication of a hypoconulid. There is a distinct, elevated crest crossing from the base of the entoconid to the posterior corner of the ectolophid. As in CM 15345, there is no mesostylid but rather a deep notch between the entoconid and the metaconid, leaving the trigonid basin open internally. It is possible that the smaller, squarer molar represents an  $M_1$ , and the second tooth an  $M_2$ , but the amount of variation in occlusal pattern seems to argue against this interpretation. The  $M_3$  shows a small, enclosed trigonid basin, or pit, and a greatly expanded posterior margin, or posterolophid, which passes into the base of the entoconid. There is a very low crest from the entoconid to the ectolophid.

## MEASUREMENTS IN MM., ISCHYROMYID SPP.

		a-p	tr	tr
CM 16014	LP <sup>4</sup>	2.65	3.20	...
CM 15352	RM <sup>1</sup> or <sup>2</sup>	2.80	3.20	...
CM 18232	LM <sup>1</sup> or <sup>2</sup>	2.85	3.30	...
CM 16084	RM <sup>3</sup>	2.70	2.50	...
	RM <sup>3</sup>	2.80	2.65	...
	RM <sup>3</sup>	3.10	2.95	...
CM 16073	RM <sup>1</sup> or <sup>2</sup>	2.65	2.70	2.60
CM 15345	RM <sup>1</sup> or <sup>2</sup>	2.95	3.20	3.15
CM 15344	RM <sup>3</sup>	2.80	2.70	2.55

**AFFINITIES:** These teeth are different from those of any other ischyromyid known from the Badwater localities. They do not match any of the material known from the late Eocene of California or Utah. As there is not enough material to determine whether there are relationships to other ischyromyids, and as there is no certainty that these teeth represent a single species, no generic allocation can be made at present.



### **Spurimus<sup>1</sup>, new genus**

TYPE: *Spurimus scottii*<sup>2</sup>, new species

DIAGNOSIS: Small ischyromyid; hypocone large on M<sup>1</sup>-M<sup>2</sup>, absent on P<sup>4</sup>; anterior cingulum narrow, low on P<sup>4</sup>-M<sup>3</sup>; metaloph generally incomplete ending in small metaconule; trigonid basin small but completely enclosed on M<sub>1</sub>-M<sub>2</sub>; notch between anterior cingulum and protoconid on M<sub>1</sub>-M<sub>2</sub>; entoconid separated from posterolophid; hypolophid complete on M<sub>1</sub>-M<sub>2</sub>.

### **Spurimus scottii<sup>2</sup>, new species**

Figures 51-64

TYPE: CM 16088, RM<sup>1</sup> or 2.

HYPODGM: P<sup>4</sup>, CM 16085; M<sup>1</sup> or 2, CM 14631, 16088, 18220, 18222, 18262, 21982; M<sup>3</sup>, CM 16022, 16075; P<sub>4</sub>, CM 16015, 21966, 21967, 21968, 21969; M<sub>1</sub> or 2, CM 14629, 14835, 16766, 18233, 21970-21974, 25351; M<sub>3</sub>, CM 21975.

DISTRIBUTION: Type from the Wood locality. All other specimens from the Wood or Rodent localities.

DIAGNOSIS: Hypocone smaller than in *Spurimus selbyi*; trigonid basin smaller, metalophid shorter, and hypolophid lower than in *S. selbyi*.

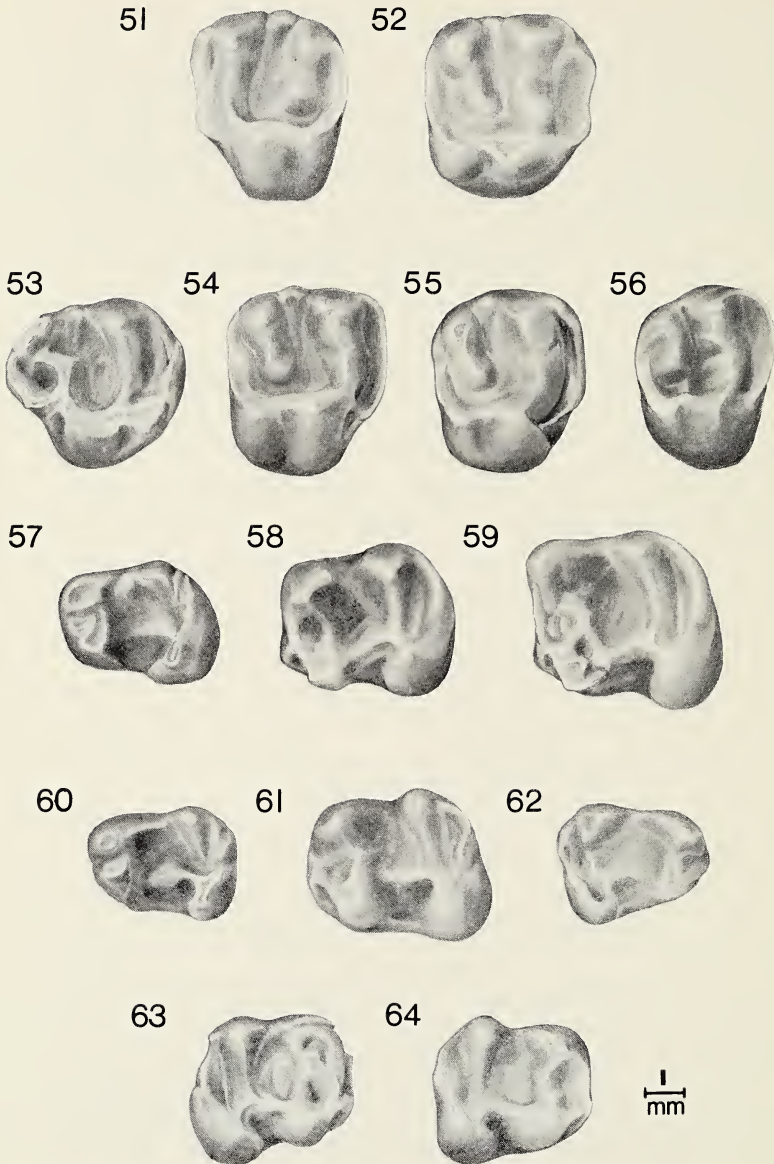
DESCRIPTION: The fourth upper premolars are similar in occlusal pattern to the first and second upper molars. They differ primarily in the absence of the hypocone on P<sup>4</sup> and in having a shorter anterior cingulum. The protocone of P<sup>4</sup> is rather elongate antero-posteriorly, so that the occlusal outline of the premolar is similar to that of M<sup>1</sup>-M<sup>2</sup>. On one P<sup>4</sup> (CM 16086) the protoconule is distinct within the protoloph. On the other P<sup>4</sup> there is no indication of a protoconule. On both teeth the metaconule is large, equaling the metacone in size. The metaloph is complete on both P<sup>4</sup>s but connected to the protocone only by a very slender, low crest.

All upper M<sup>1</sup>-M<sup>2</sup>s have a large separate hypocone set off from the protocone by a distinct groove down the internal face of the teeth. The anterior cingulum on M<sup>1</sup>-M<sup>2</sup> is long and narrow, and lies very low on the anterior face of the teeth. The protoloph is strong and high, and shows no indication of a protoconule. The metaloph is generally incomplete, ending in a distinct metaconule which is separated from the inner face of the protocone. The valley between the protoloph and the metaloph is deep and is open buccally. On some specimens there is a very small mesostyle at the buccal end of the central valley. The central valley is directed diagonally across the tooth, following the diagonal slope of the metaloph.

<sup>1</sup>[L., fr. *spurius* false + *mus* mouse.] False mouse.

<sup>2</sup>For the late "Scotty" Hendry, who founded the Clear Creek Cattle Company of Badwater, Wyoming.





Figs. 51-64. *Spurimus scottii*. 51. CM 18220, LM<sup>1-2</sup>. 52. CM 14631, RM<sup>1-2</sup>. 53. CM 16075, RM<sup>3</sup>. 54. CM 16088, RM<sup>1-2</sup>, Type 55. CM 21982, RM<sup>1-2</sup>. 56. CM 16085, RP<sup>4</sup>. 57. UCM 21968, LP<sup>4</sup>. 58. CM 21970, LM<sub>1-2</sub>. 59. CM 21971, LM<sub>1-2</sub>. 60. CM 21967, LP<sup>4</sup>. 61. CM 14835, LM<sub>1-2</sub>. 62. CM 16015, RP<sup>4</sup>. 63. CM 21974, RM<sub>1-2</sub>. 64. CM 16766, RM<sub>1-2</sub>.

Third upper molars are nearly circular in occlusal outline, but show a slight notch between the protocone and the postero-external corner of the teeth. There is also an expansion anterior to the protocone where the anterior cingulum curves to come into the protocone slope. There is no distinct metaconule on  $M^3$  but there is a loph which passes from the posterior corner of the protocone into the talonid basin. This loph then forks, one arm passing posteriorly to the postero-external corner of the tooth. The other arm passes directly externally to the buccal side of the tooth. Consequently there are two small, shallow basins that lie between the loph and the slightly elevated postero-external margin of the tooth.

The lower fourth premolars are all long, slender teeth with relatively simple occlusal patterns. The anterior half of the tooth is essentially a single, high ridge with protoconid and metaconid almost completely fused. In unworn specimens there is a very shallow, ephemeral trigonid basin visible, but this is soon obliterated with wear. The posterior slope of this high ridge passes evenly down into the talonid basin, with no break in the region of the ectolophid and no indication of a mesostylid. The hypoconid and entoconid are both rather small, low cusps on  $P_4$ , and the posterolophid is only slightly elevated above the level of the trigonid basin. On one specimen (CM 16015) there is a distinct hypoconulid in the center of the posterior border of  $P_4$ . This cusp is connected by a low ridge to the entoconid. In other specimens this low ridge into the posterolophid is visible, but there is no distinct hypoconulid present.

The molars are considerably larger than the  $P_4$ s, but they also show the elongate, rather slender form. The trigonid basin is a small pit, distinct and rather deep, enclosed between the anterior cingulum and the metaconid, which is complete on all  $M_1$ - $M_2$ s. There is a shallow notch between the anterior cingulum and the anterior face of the protoconid. The anterior cingulum is somewhat swollen, giving the appearance of an incipient anteroconid. The apex of the metaconid rises considerably higher than the tops of any of the other cusps, and there is a very high, steeply sloping, posterior metaconid surface. The ectolophid is rather low on all lower molars and there is no indication of a mesoconid. The posterolophid is elevated from the hypoconid through the region of the hypoconulid, then drops abruptly to pass into the base of the entoconid at the postero-external corner of that cusp. The entoconid is thus set off from the posterolophid, and there is a long narrow valley between the entoconid, hypolophid, and posterolophid. A hypolophid is well developed in all cases from the posterior corner of the ectolophid. There is only one half of an  $M_3$  preserved, but this shows the hypolophid distinctly.

The buccal valley on the lower molars between the protoconid and the hypoconid is long anter-posteriorly, but very shallow.

MEASUREMENTS IN MM., *Spurimus scottii*

		N	M	OR	M <sub>W</sub> (N)	M <sub>R</sub> (N)
P <sup>4</sup>	a-p	2	1.95	1.81-2.12	1.95(2)	...
	tr	2	2.43	2.25-2.62	2.43(2)	...
M <sup>1</sup> or <sup>2</sup>	a-p	6	2.06	1.94-2.12	2.09(4)	2.03(2)
	tr	6	2.50	2.37-2.75	2.51(4)	2.47(2)
M <sup>3</sup>	a-p	2	2.25	2.25	2.25(2)	...
	tr	2	2.22	2.19-2.25	2.22(2)	...
P <sub>4</sub>	a-p	5	1.77	1.69-1.81	1.77(5)	...
	tr	5	1.24	1.19-1.25	1.24(5)	...
	tr	5	1.45	1.37-1.56	1.45(5)	...
M <sub>1</sub> or <sub>2</sub>	a-p	10	2.18	2.00-2.44	2.11(5)	2.25(5)
	tr	10	1.73	1.50-2.12	1.67(5)	1.80(5)
	tr	10	1.95	1.69-2.31	1.89(5)	2.01(5)
M <sub>3</sub>	a-p	0	...	...	...	...
	tr	0	...	...	...	...
	tr	1	2.00	...	2.00(1)	...

**AFFINITIES:** *Spurimus scottii* seems to be most closely related to the prosciurine ischyromyids. Within the prosciurines there has been a tendency to enlarge the talonid basin and to develop discrete cusps and short crests along the internal and external margins of this basin. Thus, in *Prosciurus*, *Cedromus*, and *Pelycomys*, the entoconid and the mesostylid are discrete cusps, with short-to-moderately elongate crests that extend into the talonid basin from these cusps. Buccally the hypoconid and the mesoconid also are discrete, sharp cusps. Correlated with the enlargement of the talonid basin is the reduction in size of the trigonid basin and the metalophid. In the upper dentition there has been a loss of the hypocone and antero-posterior compression of the protocone, so that the inner border of the upper cheek teeth is rather short, giving the teeth a triangular occlusal outline.

This type of dentition could have been derived from that of *Spurimus scottii* through reduction and loss of some structures seen in that species. There could have been reduction and shortening of the hypolophid, reduction in the size of the metalophid and trigonid basin, and reduction and eventual loss of the hypocone in the upper molars. The antero-posterior elongation of the lower molars seen in *Spurimus scottii* is similar to the condition found in the Oligocene prosciurines. If *Spurimus scottii* evolved from *Spurimus selbyi* of locality 5, then selection was acting to bring about the type of reduction mentioned above. Between *S. selbyi*



and *S. scottii* this would include reduction in importance and size of the hypocone, and in the lower molars, reduction in the size of the trigonid basin and in the height and importance of the hypolophid. Thus, if this is a natural, phyletic sequence, continuation of these trends would lead easily into the Oligocene prosciurines. If, however, the sequence *Spurimus selbyi* to *Spurimus scottii* is invalid, then neither of these species has any direct relationship to the Oligocene prosciurines.

### *Spurimus selbyi*<sup>1</sup>, new species

Figures 65-73

TYPE: CM 15424, LM<sup>1</sup> or 2.

HYPODIGM: Type and P<sup>4</sup>, CM 14511, 15566, 15570, 15571; M<sup>1</sup> or 2, CM 15333, 15334, 15336, 15567; dP<sub>4</sub>, CM 15572, 18236; P<sub>4</sub>, CM 14784, UCM 24742; M<sub>1</sub> or 2, CM 14783, 15335, 25350, UCM 24730, 24734, 24767, 24801; M<sub>3</sub>, CM 14785.

DISTRIBUTION: All specimens from localities 5 and 5A.

DIAGNOSIS: Hypocone large; anterior cingulum on P<sup>4</sup>-M<sup>2</sup> high; trigonid basin large; hypolophid strong.

DESCRIPTION: The fourth upper premolars are generally rather triangular in occlusal outline, with antero-posteriorly compressed protocone, no hypocone, and a large, elevated parastyle. The protoloph of P<sup>4</sup> is complete, with only a faint indication of the protoconule within it. The metaloph is generally incomplete, ending in a large distinct metaconule which is subequal to the metacone. The metaconule and metacone are joined by a thin crest. One P<sup>4</sup> (CM 15570) shows a thin connection between the metaconule and the protocone. A mesostyle is present, but is very small and fused into the postero-external side of the paracone.

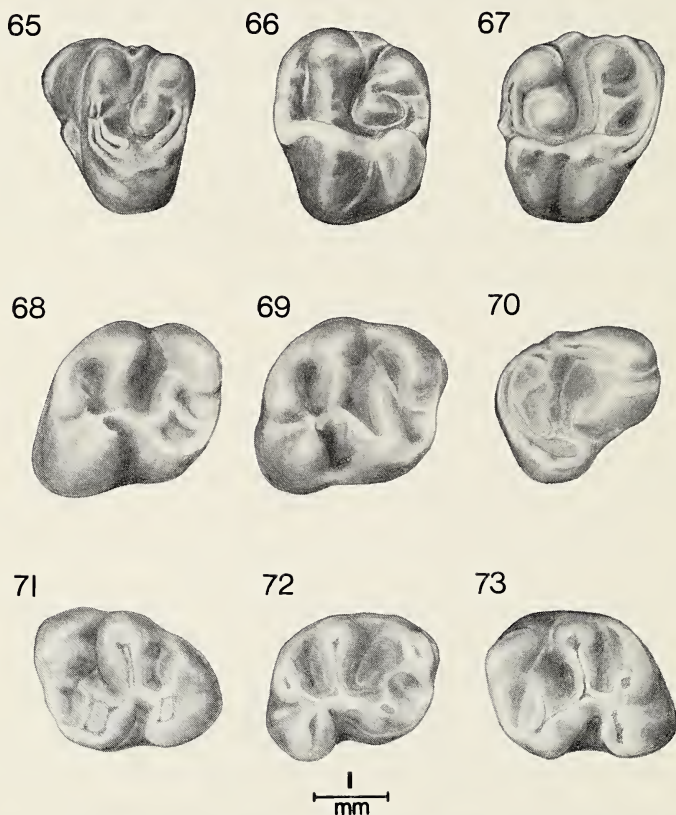
The first and second upper molars are square in occlusal outline, with a large distinctive hypocone that is generally set off from the protocone by a deep, lingual groove. The anterior cingulum is wide and the anterior margin of the cingulum is raised into a thin, high crest. There is a rather deep but narrow valley enclosed between the anterior crest and the protoloph. The protoloph is high but very thin and there is little, if any, swelling in the region of the protoconule. All five M<sup>1</sup>-M<sup>2</sup>s display incomplete metalophs. The metacone and metaconule are subequal in size and are joined by a very thin ridge. The posterior cingulum is short, passing from the hypocone into the postero-internal base of the metacone.

The deciduous P<sub>4</sub> is an extremely thin, elongate tooth with only a shallow notch between the protoconid and metaconid. The postero-

<sup>1</sup>Named for Merrill Selby, proprietor of the Big Horn Hotel of Arminto, Wyoming.



lophid is high and thin, and a very shallow, narrow valley lies between the posterolophid and ectolophid. The entoconid is separated from the posterolophid and there is a low, thin crest passing from the entoconid to the posterior end of the ectolophid.



Figs. 65-73. *Spurimus selbyi*. 65. CM 14511, LP<sup>4</sup>. 66. CM 15424, LM<sup>1-2</sup>, Type. 67. CM 15334, RM<sup>1-2</sup>. 68. CM 14783, RM<sup>1-2</sup>. 69. UCM 24767, RM<sup>1-2</sup>. 70. CM 18236, RdP<sub>4</sub>. 71. CM 14785, LM<sub>3</sub>. 72. CM 25350, RM<sub>1-2</sub>. 73. CM 15335, LM<sub>1-2</sub>.

The fourth lower premolars resemble M<sub>1</sub>-M<sub>2</sub> closely except in the protoconid-metaconid relation. On P<sub>4</sub> these two cusps are set close together, and the trigonid basin is reduced to a mere notch, directed antero-posteriorly between them. The posterior half of P<sub>4</sub> resembles that of M<sub>1</sub>-M<sub>2</sub> described below.

The lower first and second molars are long in relation to their width. They are cusate, and the lophids are extremely thin, although high. Anteriorly, the trigonid basin is large and rather deep, and is enclosed both anteriorly and posteriorly. The protoconid, metaconid, hypoconid, entoconid, and hypoconulid are all high, rather sharp cusps projecting above the level of the lophs. The ectolophid is well developed in all cases, as is the hypolophid, which meets the ectolophid at its posterior corner. There are deep valleys between the posterior slope of the metaconid and the hypolophid, and again between the hypolophid and posterolophid. Both valleys open lingually. There is no mesostylid or mesoconid.

The third lower molar shows essentially the same structure as  $M_1$ - $M_2$  except that the hypoconid-hypoconulid area is more rounded and swollen, and somewhat more distinctly separated from the entoconid.

MEASUREMENTS IN MM., *Spurimus selbyi*

		N	M	OR
P <sup>4</sup>	a-p	4	1.85	1.75-2.00
	tr	4	2.33	2.10-2.60
M <sup>1</sup> or <sup>2</sup>	a-p	5	2.08	2.00-2.15
	tr	5	2.44	2.30-2.55
dP <sub>4</sub>	a-p	2	2.17	2.15-2.20
	tr	2	1.30	1.30
	tr	2	1.72	1.65-1.80
P <sub>4</sub>	a-p	2	2.32	2.25-2.40
	tr	2	1.52	1.50-1.55
	tr	2	1.90	1.80-2.00
M <sub>1</sub> or <sub>2</sub>	a-p	7	2.23	2.10-2.40
	tr	7	1.84	1.65-2.10
	tr	7	2.11	1.95-2.35
M <sub>3</sub>	a-p	1	2.30	...
	tr	1	2.00	...
	tr	...	1.80	...

**AFFINITIES:** This species does not seem to be closely related to any other known ischyromyids, with the exception of *Spurimus scottii* discussed earlier. It differs from *Spurimus scottii* in having a stronger hypocone on the upper molars and a much higher anterior cingulum or anterior crest than does *Spurimus scottii*. In the lower molars, the trigonid basin is larger; the cusps are generally sharper, higher, and more distinct; and the talonid basin is much smaller, than in the species from the Wood locality. *Spurimus selbyi* was probably ancestral to *Spurimus scottii*.

## DISTRIBUTION OF ISCHYROMYIDS AT BADWATER

It now appears that there actually is an age difference between various late Eocene localities on Badwater Creek. Table 1 shows the distribution of ischyromyid species among five of these localities. Localities 5 and 6 have a similar species association—quite distinct from that found at the Wood and Rodent localities. There appears to be only one species common to these two groupings: *Microparamys dubius*, which is found at the Wood locality as well as at 5 and 6. In two instances, species found at localities 5 and 6 are ancestral to populations found at the Wood and Rodent localities. The population described as *Leptotomus* near *L. guildayi* from 5 and 6 is somewhat more primitive than *Leptotomus guildayi* found at the Wood and Rodent localities. In the other instance, the species *Spurimus selbyi* from localities 5 and 6 is clearly distinct from, but ancestral to, *Spurimus scottii* of the Wood and Rodent localities. Two genera found at localities 5 and 6 are not represented at the Wood and Rodent localities: *Ischyrotomus* and *Rapamys*. Several specimens of the advanced ischyromyid ?*Ischyromys* have been recovered from the Wood and Rodent localities but there has been no suggestion of the presence of this form at the other localities.

Table 1: Distribution of Ischyromyids at Badwater

Localities	5	5A	6	W	R
<u>Ischyrotomus</u> cf. <u>I. eugenei</u>	X				
<u>Leptotomus</u> <u>guildayi</u>				X	X
<u>Leptotomus</u> near <u>L. guildayi</u>	X	X	X		
<u>Rapamys</u> <u>wilsoni</u>	X	X	X		
<u>Spurimus</u> <u>selbyi</u>	X	X			
<u>Spurimus</u> <u>scotti</u>				X	X
<u>Ischyromys</u> sp.				X	X
<u>Microparamys</u> <u>dubius</u>	X	X	X	X	
<u>Ischyromyid</u> sp.				X	X

The ischyromyids then, clearly indicate that localities 5 and 6 have a somewhat older fauna than that found at the Wood and Rodent localities. This age difference was suggested earlier (Black, 1970; Dawson, 1970) by the distribution of cylindrodont rodents and by the presence of different species of *Mytonolagus* at the two sets of localities. Some of the



differences noted in total faunal composition between these sets may have been ecologically controlled. However, the ancestor-descendant relationship between species of *Leptotomus* and *Spurimus* certainly indicates that an age difference is also responsible for some of the differences in composition.

#### DISTRIBUTION OF NORTH AMERICAN LATE EOCENE ISCHYROMYIDS

At first glance the distribution pattern of ischyromyid species and genera among the main late Eocene localities in North America is confusing. Upon closer scrutiny, however, several trends are observable. I have considered here only the well-known late Eocene faunas from Southern California, the Uinta Basin in Utah, and the Badwater localities. Work being done by others on the late Eocene faunas of the Big Bend area in Texas and the Washakie Basin in Wyoming, and our studies in Montana, may modify these patterns somewhat, but I doubt that they will be changed significantly.

On the species level very little can be learned, for each geographic area seems to have its own distinct species complexes. Out of some twenty-four species belonging to 10 genera, there are only two species common to any two of these geographic areas. *Microparamys dubius* is found at Badwater and the Uinta Basin, but not in California. *Ischyrotomus eugenei* is found at Badwater and the Uinta Basin. Because of the specific endemism in these three areas, it is much more profitable to look at the distribution of genera. When this is done, several patterns emerge.

First, three genera, *Leptotomus*, *Ischyrotomus*, and *Microparamys*, are found in all three geographic areas. Two of these genera are the least specialized of all late Eocene ischyromyids. In this regard, *Leptotomus* and *Ischyrotomus* might be considered the late Eocene counterparts of the modern *Sciurus*, showing little variation in dental morphology over a wide geographic area. The third genus, *Microparamys*, found in all three areas, is somewhat more specialized, particularly in its dentition. However, this group had a long history pre-dating the late Eocene, and was probably the most successful of all the small-sized ischyromyids. In this light, its wide geographic occurrence with the larger but unspecialized genera *Leptotomus* and *Ischyrotomus* is not unusual.

Genera endemic to single regions make up the second group or pattern of ischyromyid distribution. Two genera endemic to the Uinta Basin in Utah are *Thisbemys* and *Janimus*. Two other genera, ?*Ischyromys* and *Spurimus*, are found only at Badwater. Under the classification used



Table II: Late Eocene Distribution of Ischyromyids

Geographic area Faunal level	Uinta Basin			Badwater		California		
	A B	C	Randlett	5 6	W R	Poway	Tapo	Pearson
<u>Leptotomus</u>	X	X	X	X	X	X	X	
<u>Ischyrotomys</u>	X	X		X		X		
<u>Microparamys</u>	X			X			X	X
<u>Thisbemys</u>	X	X						
<u>Janimus</u>		X						
<u>Ischyromys</u>					X			
<u>Spurimus</u>				X	X			
<u>Mytonomys</u>	X	X	X				X	
<u>Reithroparamys</u>		X				X		
<u>Rapamys</u>				X		X		

here, there are no endemic genera recognized in the California late Eocene assemblages, as the genus *Uriscus* is considered to be a synonym of *Reithroparamys*, and *Tapomys* of *Leptotomus*. All four of the genera that occur in only one region are highly specialized ischyromyids. The presence of ?*Ischyromys* at the later Badwater late Eocene localities may indicate that this faunal level is somewhat younger than any of the other late Eocene occurrences.

A third and final group of genera may be recognized. This comprises those forms that are found in two of the three geographic regions, but not in the third. In this group are *Mytonomys* and *Reithroparamys*, different species of which are found in Utah and California, and *Rapamys*, with different species in California and at Badwater. Species of *Mytonomys* and *Rapamys* are highly specialized ischyromyids, and perhaps they had narrower ecological tolerances than did species of *Leptotomus* and *Microparamys*. The species of *Reithroparamys* found in California and Utah are both small forms whose dentition is not highly specialized. No members of this genus have been found at Badwater. Members of this third group may offer the best possibilities for insight into the local environments of deposition. Restricted occurrence of these genera to two of the three regions suggests the presence of other associated faunal or environmental factors that were acting to produce differing associations at each locality. Determination of local environments will require a much more detailed knowledge of the physical factors of deposition than is presently available for the localities in California and Utah.

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THE CRINOID GENUS *POLUSOCRINUS*  
IN THE AMES LIMESTONE (PENNSYLVANIAN)  
OF WEST VIRGINIA

J. J. BURKE<sup>1</sup>

INTRODUCTION

The crinoid described in the following pages represents a new species of the inadunate genus *Polusocrinus*, and this paper constitutes the first report of that genus in the Pennsylvanian of the Appalachian region.

I am indebted to Director M. Graham Netting and Dr. E. R. Eller, of Carnegie Museum, for the privilege of describing this specimen from the Carnegie Museum collection of fossil invertebrates. I also wish to thank Mr. Calvin Colson and the Geology Department of Ohio University for the photographs used for the illustrations.

SYSTEMATICS

Family Ampelocrinidae Kirk, 1942

Genus *Polusocrinus* Strimple, 1951

***Polusocrinus wellsburgensis*<sup>2</sup>, new species**

Figures 1-3

**DIAGNOSIS:** A small species of *Polusocrinus* (width of dorsal cup about 17.5 mm); cup relatively low (form ratio about 0.54) and globe-shaped; base nearly flat and tips of infrabasals scarcely showing in lateral view of the cup; basals slightly wider than long.

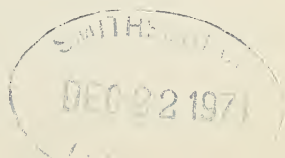
**HOLOTYPE:** A dorsal cup, CM 4975.

**OCCURRENCE:** Ames limestone, Conemaugh group, upper Pennsylvanian.

**LOCALITY:** Painters Run (Painter Hollow) near Wellsburg, Brooke County, West Virginia (lat. 40° 15' 45" N, long 80° 35' 33" W).

<sup>1</sup>Cleveland Museum of Natural History, Wade Oval, University Circle, Cleveland, Ohio 44106.

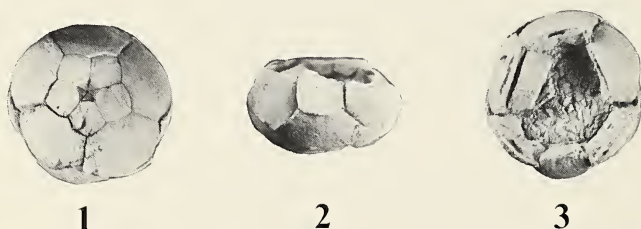
<sup>2</sup>Named for Wellsburg, West Virginia.





DESCRIPTION: Some of the cup plates of the holotype specimen have been dislocated, but it is evident that the dorsal cup was definitely constricted at the summit and consequently globe-shaped. The height is slightly more than half the width. The plates are smooth and the sutures are not impressed. The base is flattened and the infrabasals are barely visible in the side-view of the cup.

The infrabasal circlet is star-shaped. The stem impression is pentagonal in outline, with each side of the pentagon bowed inward slightly. Within the impression there are slight traces of culmina, and the tips of the infrabasals curve downward from the lumen. The outline of the lumen is indistinct, but it appears to be pentolobate. The circlet is very mildly concave in the vicinity of the impression. The plates become tangent to the basal plane about halfway between their distal tips and the borders of the impression. Beyond that point they curve gently upward.



Figs. 1-3. *Polusocrinus wellsburgensis*, new species. Holotype, CM 4975, from the Ames limestone, Conemaugh group, Brooke County, West Virginia. 1. dorsal view. 2. posterior view. 3. ventral view. x1.

The five basals are moderately convex and hexagonal, except for the posterior, which is truncated for reception of the anal plate and is consequently heptagonal. These plates are a little wider than they are long, and none of them is as widely expanded as the infrabasal circlet.

The radials are slightly convex and a little more than two-thirds as long as they are wide. The length of an interrarial suture is slightly more than half the greatest length of the plate. The greatest width of these plates is at the proximal lateral corners, where the distal extremities of the basals meet the interrarial sutures. Although these plates are now displaced, their short widths at the summits indicate constriction of the cup distally.

In ventral view, the radials are broadly arcuate in external outline. The outer marginal ridge is also arcuate. The external ligament pit

extends as a relatively wide slit that occupies about one-fourth of the width of the articular surface, and is fairly deep. The transverse ridge is distinct, but (probably because of wear) shows no denticulations. The ridge is fairly straight and does not conform to the bowed external outline of the plate. In consequence it does not extend to the lateral margin of the radial.

The inner articular surfaces of the radials do not preserve much detail. They slope inward, which is characteristic of the genus, forming two low, slightly concave lobes separated by a V-shaped intermuscular notch and a shallow intermuscular groove. There are also indications of shallow oblique fossae.

The anal plate is relatively large, quadrangular, and slightly longer than it is wide. The greatest width is above the middle. The distal surface has been damaged, and the facets for articulation with additional anal plates are not preserved.

The left anterior first primibrach has fallen into the body cavity, but its articular surface is still in contact with that of the right anterior radial. The plate is quadrangular, more than  $2\frac{1}{2}$  times wider than it is long, and narrows distally. It is broadly arcuate in outline proximally, but becomes strongly convex from side to side in its distal reaches. There is a prominent outer ligament pit, corresponding to that of the radial, on the outer surface of the proximal articular facet. The distal articular face is smooth.

Linear measurements in millimeters of the holotype specimen of *Polusocrinus wellsburgensis* (C.M. 4975) are as follows:

Width (estimated) of dorsal cup .....	17.5
Height (estimated) of dorsal cup .....	9.5
Ratio of height to width .....	ca. 0.54
Maximum width of infrabasal circlet .....	9.5
Width of stem impression .....	2.8
Width of left anterior basal .....	8.8
Length of left anterior basal .....	8.1
Length of suture between basals .....	4.5
Greatest width of left anterior radial .....	9.4
Width of left anterior radial at summit .....	8.1
Length of left anterior radial .....	6.0
Length of suture between radials .....	3.5
Width of anal plate .....	5.2
Length of anal plate .....	5.4
Width (estimated) of left anterior first primibrach .....	7.5
Length of left anterior first primibrach .....	2.8

## DISCUSSION

In general proportions the dorsal cup of *Polusocrinus wellsburgensis* resembles that of *Polusocrinus ochelataensis* Strimple, 1952. The ratio of height to width (about 0.54) approximates that of the holotype of Strimple's species. *Polusocrinus ochelataensis* is found in the Wann formation, upper Missourian, of Oklahoma. Most authorities tend to regard the Ames limestone, from which *Polusocrinus wellsburgensis* is derived, as also of upper Missourian age, but as somewhat younger than the Wann.

The Ames species differs from *Polusocrinus ochelataensis*, however, in being a smaller form, in showing basals that are slightly wider than they are long, and in having a flatter base. These characteristics, together with the slight exposure of the infrabasals in lateral view and the constriction of the cup at the summit of the radials should serve to distinguish *Polusocrinus wellsburgensis* from other species that have been attributed to the genus.

The holotype of *Polusocrinus wellsburgensis* is, to my knowledge, the only representative of the genus that has ever been collected from the Pennsylvanian of the Appalachian region. The specimen has been in the collection of Carnegie Museum for over forty years, and at one time (Burke, 1930) I identified it as *Graphiocrinus* sp.

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THE BUTTERFLIES OF THE GENERA *SIPROETA*  
AND *METAMORPHA* (LEPIDOPTERA: NYMPHALIDAE)

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ACKNOWLEDGEMENTS

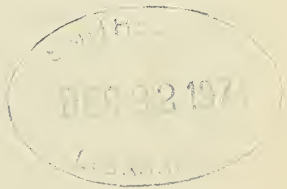
After the death of the senior author this paper was completed by F. Martin Brown, Research Associate, and prepared for publication by the late Jean W. (Mrs. Richard M.) Fox, Research Assistant; George E. Wallace, Curator; and Harry K. Clench, Associate Curator, all of the Section of Insects and Spiders, Carnegie Museum. The drawings of wing venation, forelegs, and genitalia (Plates 1-4) were prepared by Richard T. Satterwhite; the photographs (Plates 5 and 6) are by Leo T. Sarnaki. Specimens were examined from the following collections (designated by abbreviations in the text): British Museum (Natural History), London, England (BM); Carnegie Museum, Pittsburgh, Pa. (CM); private collection of Herman G. Real, San Mateo, Calif. (F); Lyman Entomological Museum, Macdonald College, McGill University, Montreal, Quebec (L); National Museum of Natural History, Washington, D. C. (USNM). The study was assisted by NSF Grant GB-5682 to the late Richard M. Fox.

PREFATORY NOTE

[At the time of Dr. Fox's death, the manuscript for this paper was practically completed. A note listing seven items to be done was on Fox's desk. I have carried out that work, which in no way alters the authorship of the paper. The principal tasks were nomenclatorial: designation of a lectotype for *Victorina steneles insularis* Holland and a neotype for *Papilio sulpitia* Stoll (not Cramer). I selected the required lectotype. I found it unwise to designate the neotype although the taxonomic and nomenclatorial support for the designation had already been supplied by Fox and Forbes. — F. M. BROWN.]

<sup>1</sup>Deceased April 25, 1968.

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## INTRODUCTION

The general use of *Victorina* for the butterflies under discussion here originated in Doubleday, Westwood, and Hewitson's *Genera of Diurnal Lepidoptera* (1846-1852), written at a time when zoologists more or less freely used generic names that appealed to them, without consideration of priority, and long before the type species concept was introduced. This monumental work carried so much prestige among lepidopterists that the names used in it were employed by authors for many years. Accordingly, *Victorina* is used in Herrich-Schäffer's *Prodromus* (1864-1865), in Staudinger's *Exotische Tagfalter* (1884-1888), in Schatz's *Familien und Gattungen* (1885-1892), in Seitz's *Grossschmetterlinge* (1914), and in other works during this period. The only variation is found in Godman and Salvin (1879-1901), who misinterpreted the significance of the male genitalia and used *Victorina* only for *stelenes*, assigning the other two Central American species to *Amphirene*.

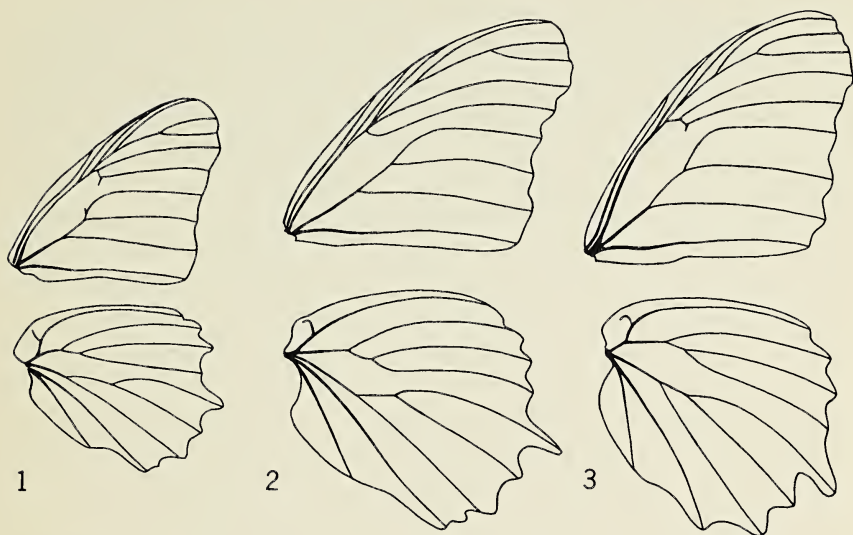
## COMPARISON OF METAMORPHA AND SIPTROETA

The butterflies formerly referred to *Victorina* Blanchard belong in two distinct genera: *Metamorpha* Hübner, containing only *M. elissa*, and *Siproeta* Hübner, containing the other three species. Both *Victorina* Blanchard and *Amphirene* Doubleday are junior synonyms of *Siproeta*.

*Metamorpha* and *Siproeta* are separated by numerous morphological characters, as follows:

VENATION (Plate I): In *Metamorpha* the third discocellular cross vein of the forewing is represented by a vestige of its anterior end at the juncture of the second discocellular with the second median branch, and by a vestige of its posterior tip on the base of the third median branch (Pl. I, fig. 1). In *Siproeta* the vestige of the posterior tip of the third discocellular is always absent (Pl. I, fig. 2). The vestige of the anterior tip is present only in *S. stelenes* (Pl. I, fig. 3). In *Metamorpha* both the second discocellular cross vein and the third median branch are shorter than in any of the *Siproeta* species. On the hind wing the humeral vein curves distad in *Metamorpha*, but curves proximad in all three species of *Siproeta*.

MALE FORELEG (Pl. II, fig. 1, *Siproeta*; fig. 2, *Metamorpha*): In *Siproeta* the tarsus is a little more than one-half the length of the tibia, and clearly is divided by a septum, representing vestigial subsegmentation, into a shorter proximal part and a longer distal part. The tibia is two-thirds the length of the femur (Pl. II, fig. 1). In *Metamorpha* the tarsus is re-



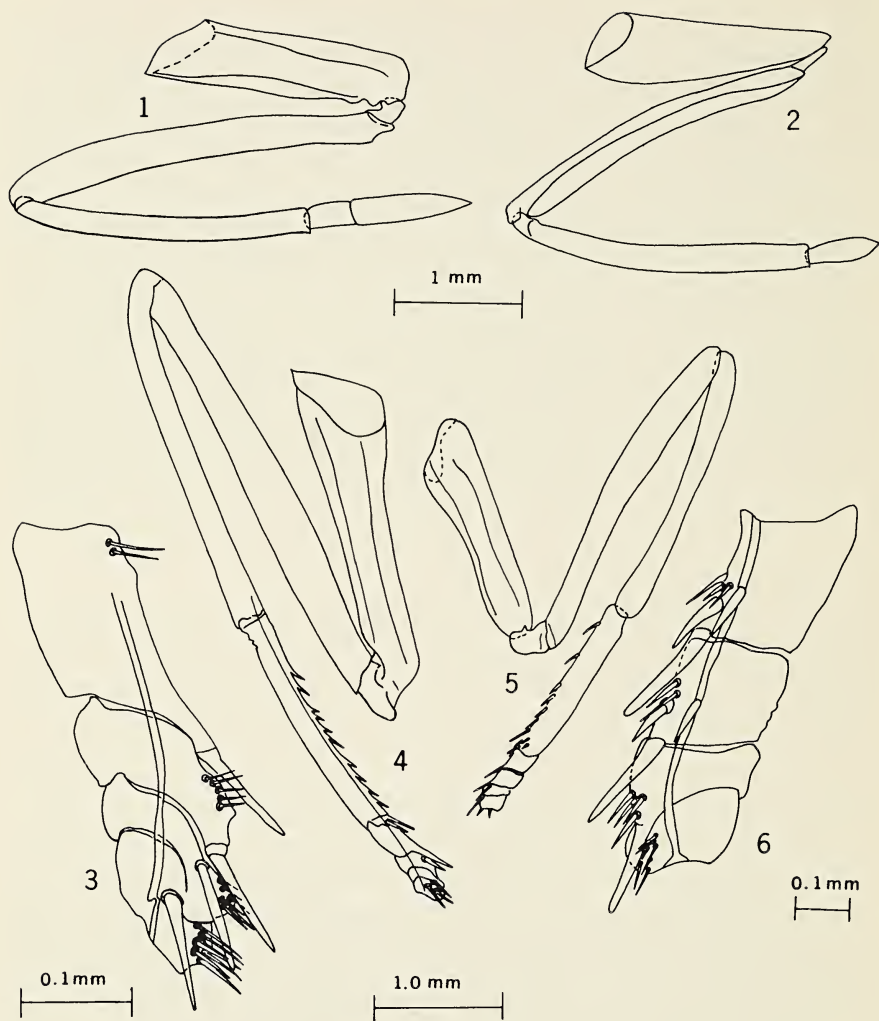
## PLATE I

Fig. 1. Venation of *M. elissa* Hübner.Fig. 2. Venation of *S. epaphus* Latreille.Fig. 3. Venation of *S. stelenes* Linné.

duced to a single elongated oval piece that is one-fourth the length of the tibia. The tibia is only slightly shorter than the femur (Pl. II, fig. 2).

**FEMALE FORELEG** (Pl. II, figs. 3, 4, *Siproeta*; figs. 5, 6, *Metamorpha*): Structure is identical in the two genera, which have enlarged spines on the second, third, and fourth tarsal subsegments. The post-tarsus is reduced to a cup-like depression on the tip of the fifth, to which the post-tarsal tendon runs. The difference in reduction of the female foreleg between the two genera is shown by the proportionate lengths of the segments: in *Siproeta* the tarsus is shorter than the coxa, the tibia is the same length as the coxa, and the second tarsal subsegment is nearly twice the length of the third (Pl. II, figs. 3, 4). In *Metamorpha* the tarsus is a little longer, and the tibia is much longer, than the coxa. The second and third tarsal subsegments are the same length (Pl. II, figs. 5, 6).

**MALE GENITALIA:** In most groups of butterflies, characters of the male genitalia distinguish species, but reliance on these characters at the generic level may result in excessive splitting. Once a generic concept has been formed on external characters, however, it generally is possible



## PLATE II

Fig. 1. Male foreleg of *S. stelenes* Linné.

Fig. 2. Male foreleg of *M. elissa* Hübner.

Fig. 3. Female tarsal joints 2-5 of *S. stelenes* Linné.

Fig. 4. Female foreleg of *S. stelenes* Linné.

Fig. 5. Female foreleg of *M. elissa* Hübner.

Fig. 6. Female tarsal joints 2-5 of *M. elissa* Hübner.



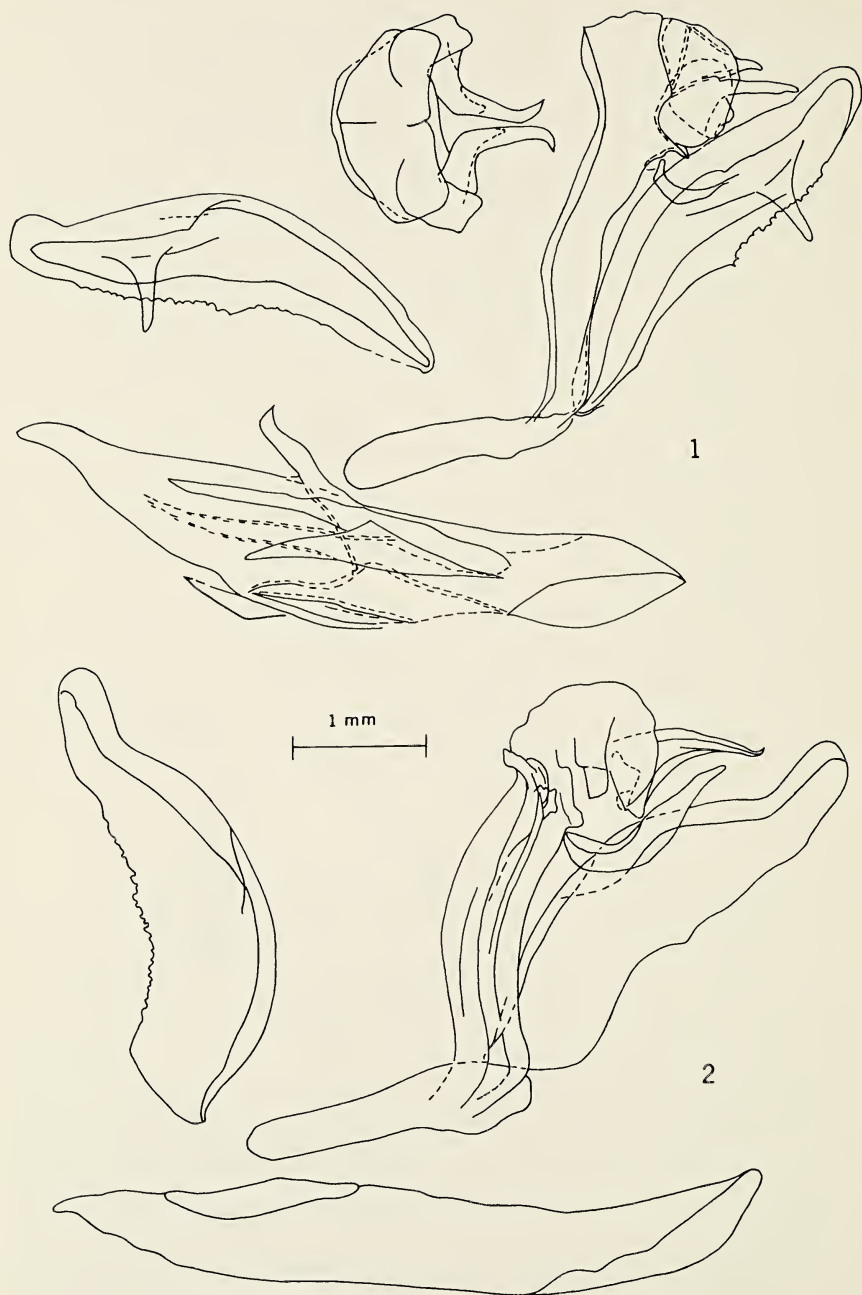
to identify some genitalic characters that are constant within the genus. The general shape of the valves serves to separate *Siproeta* and *Metamorpha*. In *Metamorpha* the valve is ovoid to rhomboid in general shape, and the posterior margin bears three large projections, one at the apex, one at the lower corner, and the other between them. The costal margin is evenly convex (Pl. IV, fig. 2). In *Siproeta* the valve is elongated and narrow, its apex bearing a large rounded projection curving upward to give the costal margin a concave contour. The posterior margin bears no projections, but curves steeply back toward the saccus (Pl. III, figs. 1, 2; Pl. IV, fig. 1). The differences in the penis-form that Godman and Salvin (1883: 281) emphasized when they separated *stelenes* (Pl. IV, fig. 1) from *epaphus* (Pl. III, fig. 1) and *superba* (Pl. III, fig. 2) do not correlate with the generic differences. On the contrary, each of the four species of these two genera has a different form of penis, and it is evident that this is a specific rather than a generic character. A difference in development of the tegumen-uncus further differentiates *Metamorpha*, which has these two parts fully fused, from *Siproeta*, which has them separated by a well developed suture.

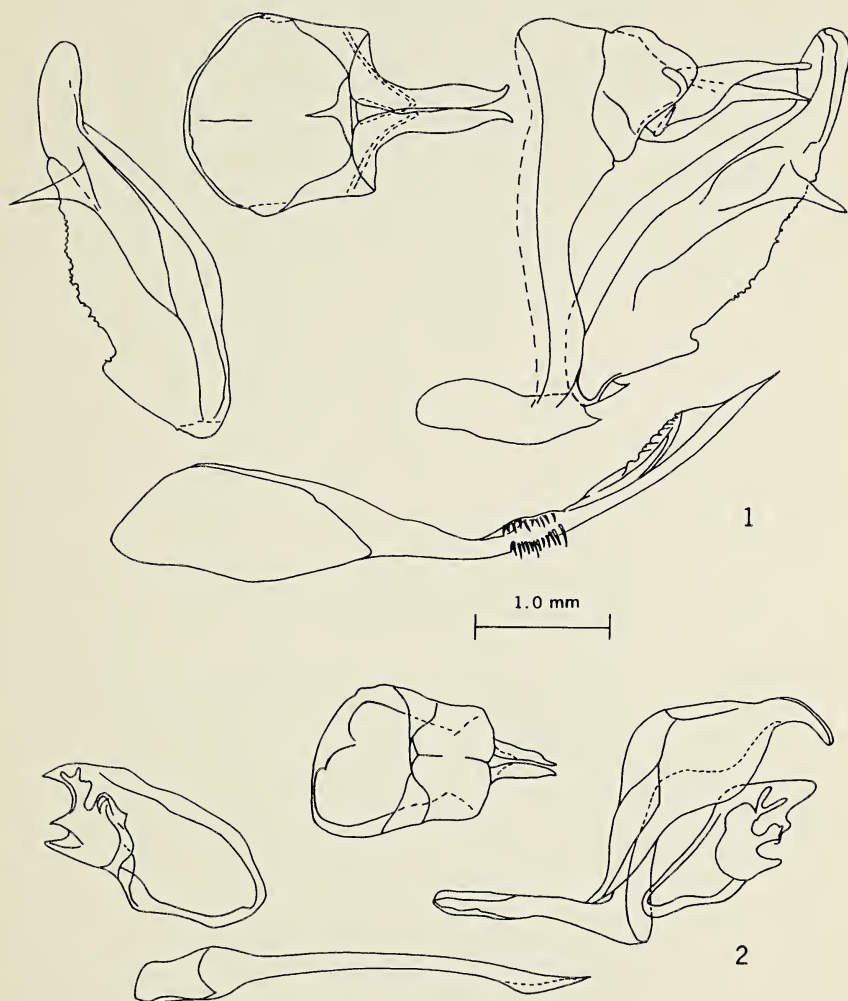
The evidence of the male and female forelegs and of the level of reduction of venation all suggest that, while *Siproeta* and *Metamorpha* are closely related and doubtless evolved from a common stem, *Metamorpha* is a little more modified. This view is supported by the male genitalia: in *Siproeta* the tegumen and uncus are still separated by a suture, but in *Metamorpha* the suture has been lost.

#### KEY TO THE SPECIES AND SUBSPECIES OF *Metamorpha* AND *Siproeta*

1. Outer margin of forewing evenly curved from apex to anal angle; no white fringe spots between the veins on either wing; no blue markings at the end of the cell on the under side of the forewing .....(*Metamorpha elissa*) 2
- Outer margin of forewing deeply scalloped between the veins; both wings with white fringe spots between the veins; blue markings present at the end of the cell on the under side of the forewing .....(*Siproeta*) 3
2. Upper side of forewing with the white median band about as wide as the dark coloring between it and the outer margin; all markings on the under side sharp and clean-cut; a silvery white band between the marginal band of the forewing and the black-brown edging of the orange post-median band . . . *M. elissa elissa*
- Upper side of forewing with the white median band narrower than the dark coloring between it and the outer margin; all markings on the under side dilute and smudged; band between the marginal lines and the postmedian band greenish or ochre; white, if present, confined to small areas near the apex and the anal angle ..... *M. elissa pulsitia*



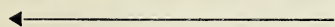




## PLATE IV

Fig. 1. Male genitalia of *S. stelenes* Linné.

Fig. 2. Male genitalia of *M. elissa* Hübner.



## PLATE III

Fig. 1. Male genitalia of *S. epaphus trayja* Hübner.

Fig. 2. Male genitalia of *S. superba* Bates.

(KEY, *Metamorpha* AND *Siprocta*, CONTINUED)

3. Upper side with a continuous white-to-creamy band crossing both wings . . . . 4  
     Upper side with numerous prominent separated light-green spots and bands . .  
     . . . . . (*S. stelenes*) 8
4. Under side of forewing with a band of black-encircled blue dots crossing the  
     middle of the cell, in addition to the similar series at the end of the cell . . . .  
     . . . . . (*S. superba*) 5  
     Under side of forewing with only the band of blue dots at the end of the cell,  
     none in the middle of the cell . . . . . (*S. epaphus*) 6
5. White cross-band on upper side narrower, 6 mm. or less at the costal margin of  
     the hind wing . . . . . *S. superba superba*  
     White cross-band on upper side wider, 7 mm. or more at the costal margin of  
     the hind wing . . . . . *S. superba euoe*
6. Apical half of forewing broadly orange-brown . . . . . *S. epaphus epaphus*  
     Apical half of forewing black or dark brown . . . . . 7
7. Ground color on upper side a dark, velvet black, with no light scaling near the  
     apex of the forewing, but with a series of antemarginal blue spots on the  
     hind wing from  $M_3$  to the anal angle . . . . . *S. epaphus gadoui*  
     Ground color on upper side brownish black, with some creamy scaling near  
     the apex of the forewing, but with no blue antemarginal spots on the hind wing  
     or with only some blue lines between  $Cu_2$  and the anal margin . . . . .  
     . . . . . *S. epaphus trayja*
8. Forewing discal cell with two well-developed greenish spots, one opposite the  
     base of  $Cu_1$ , the other beyond it opposite  $M_3-Cu_1$ , usually about equal in size  
     above and always distinctly present on the under side . . . *S. stelenes biplagiata*  
     Forewing discal cell with only the basal of the two greenish spots present on  
     upper and under sides, the distal one minute at most . . . . . 9
9. Greenish submedian band on upper side of hind wing distinctly narrower than  
     the dark median band; postmedian spots on under side of hind wing silvery,  
     distinctly shorter than the unicolorous marginal band beyond them . . . . .  
     . . . . . *S. stelenes sopherne*  
     Greenish submedian band on upper side of hind wing as wide as, or wider than,  
     the dark median band, which often contains a tawny partial stripe; postmedian  
     spots on under side of hind wing greenish to silvery, as wide as, or wider than,  
     the marginal area beyond them . . . . . 10
10. On under side of hind wing the dark median band (which contains a white and  
     a tawny stripe) distinctly wider than the greenish postmedian spots on the  
     upper side (which shine through their larger homologues on the under side);  
     greenish spot in  $Cu_1-Cu_2$  on upper side of forewing occupies not more than  
     the basal half of the space . . . . . *S. s. stelenes*  
     On under side of hind wing the dark median band (with white and tawny  
     stripes) not wider than the greenish postmedian spots on the upper side;  
     greenish spot in  $Cu_1-Cu_2$  on upper side of forewing covers more than the  
     basal half of the space and is longer than the area beyond it . . . . .  
     . . . . . *S. stelenes meridionalis*

## SYSTEMATIC REVIEW

Genus *Siproeta* Hübner, 1823

*Siproeta* Hübner, 1823 [1806-1838], 3: pl. 48. Type species, *Siproeta trayja* Hübner, by monotypy.

*Victorina* Blanchard, 1840: 447. Type species, *Papilo stelenes* Linné, 1758, by original designation.

*Amphirene* Doubleday, 1844: 86. Type species, *Vanessa epaphus* Latreille, 1811, designated by Scudder, 1875.

*S. trayja* and *Vanessa epaphus* are here considered subspecies of a single species, and therefore *Amphirene* is a junior objective synonym of *Siproeta*. The significance of differences in the penis was misinterpreted by Godman and Salvin [1883 (1879-1901)], which led them to separate *stelenes* from *epaphus*, and to place the former in *Victorina* and the latter in *Amphirene*. The two species are, however, congeneric, and *Victorina* is also a junior (subjective) synonym of *Siproeta*.

The diagnostic features separating *Siproeta* from *Metamorpha* were detailed above. The most significant are the male foretarsi, the hind wing humeral veins, the displacement of forewing  $M_3$ , and the tegumen-uncus of the male genitalia.

*Siproeta* comprises three species, which differ from each other only in color and pattern of the wings and in the male penis. *S. epaphus*, with three subspecies, and *S. stelenes*, with four, are both widespread in the neotropics. *S. superba*, with two subspecies, is confined to Central America.

*Siproeta epaphus*

Three subspecies are known: *S. e. epaphus*, distributed from Mexico to Peru and Bolivia, and into northern Venezuela; *S. e. gadoui*, known only from El Pão, Bolívar, Venezuela; and *S. e. trayja*, found in Paraguay and southeastern Brazil. Because *S. e. epaphus* has a large tawny-brown area over the apical half of the forewing, it has generally been treated as a species separate from *trayja*, but the two are identical in every other feature, including the structure of the pattern.

The male genitalia of *S. epaphus* differ from those of the other two species in the distinctive penis, which is thick and heavy, with four prominent finger-like projections around its middle, and in the valve, which bears a long down-pointing spine on the edge of the saccular fold.



*Siproeta epaphus epaphus* (Latreille)

*Vanessa epaphus* Latreille 1811 (1811-1832), 2: 74; pl. 35, figs. 3, 4 (Peru).

*Victorina epaphus*, of authors.

The type is a male in the Muséum National d'Histoire Naturelle, Paris.

SPECIMENS EXAMINED (total 102 ♂, 32 ♀): *Mexico*: Colima: Colima (CM). Veracruz: Jalapa (CM, USNM); Motzorongo; Santa Rosa (USNM). Tabasco: "Tabasco" (USNM). *Guatemala*: "Guatemala" (CM). Solola: Olas de Mocá; Yzabal: Puerto Barrios; Quiriguá (part as Quirguá); Quezaltenango: Volcán Santa María; (CM, USNM). *El Salvador*: "El Salvador" (CM). Lago de Coatepeque; Los Chorros (Santa Tecla); San Salvador; Santa Tecla; (CM, USNM). Not located: Ayualo; Finca Santa Marta (Ayualo); (CM). *Honduras*: "Honduras" (CM). Copán; San Pedro Sula; (CM). *Costa Rica*: Carillo; Juan Viñas; (CM, USNM). *Panama*: Cerro Campana; El Valle; (F). *Venezuela*: Dist. Federal: Caracas; (CM). Vague: "Mountains of Merida" (CM). *Colombia*: Magdalena: Bonda; Cincinnati (Sierra Nevada de Santa Marta); Hacienda Cincinnati (Sierra San Lorena); Minca; Las Nubes; Onaca; Las Taguas (Sierra Nevada de Santa Marta); (CM). Antioquia: San Andrés (Tierradentro); (USNM). Cundinamarca: Bogotá; (CM, USNM). Vague: "Mountains near Bogota" (CM). Nariño: Chambú; Río Cartagena; (CM). *Ecuador*: "Ecuador" (USNM); Tungurahua: Hacienda La Mascota (Río Topo); (CM). Chimborazo: Dos Puentes; Huigra; (CM). Oriente: Abitagua; Mera; Río Topo; (CM). *Peru*: "Peru" (CM). Amazonas; San Pedro; (CM). Cajamarca: Calendín; (CM). Junín: Satipo; (CM). Cuzco: Río Chanchosmayo (as Chanchamayó); (USNM). Not located: "La Pampa" (Río Távora). *Bolivia*: "Bolivia" (USNM). Santa Cruz: Buenavista; Portachuelo (Río Palmitillos); Santa Cruz; (CM). Prov. del Sará (CM).

*Siproeta epaphus gadoui* Masters

*Siproeta epaphus gadoui* Masters, 1967; 193-194. (El Pão, Bolívar, Venezuela).

The holotype and allotype are in Carnegie Museum (C.M. Ent. type series no. 652), with paratypes in the collections of Central University, Maracay, Venezuela, of A. Gadou, H. Skinner, and of J. H. Masters. All these specimens were taken in the vicinity of El Pão, Bolívar, Venezuela. This recently described subspecies is especially interesting in that it appears to have been derived from *trayja* stock rather than from the geographically adjacent *epaphus*, although the entire Amazon Valley now separates *trayja* and *gadoui*.

SPECIMENS EXAMINED (total 1 ♂, 1 ♀): *Venezuela*: Bolívar: El Pão; (CM).

*Siproeta epaphus trayja* Hübner

*Siproeta trayja* Hübner, [1823] (1806-1838), 3: pl. 48 (no locality cited).

The type may be in Vienna, but since the Hübner figure is definitive we have not inquired.

[The records cited below from Venezuela, Colombia, and Ecuador are all vague or otherwise unsatisfactory. Furthermore, they conflict with an otherwise consistent and cohesive pattern of distribution that shows subspecies *trayja* to be confined to southern Brazil and adjoining areas. We hold all these records of *trayja* from northern South America to be suspect until or unless confirmed by authentic captures.—H.K.C.]

SPECIMENS EXAMINED (total 31 ♂, 4 ♀): *Venezuela*: "Venezuela" (USNM). *Colombia*: "Colombia," (USNM). Cundinamarca: Bogotá; (L). *Ecuador*: Guayas: Guayaquil; (L). *Brazil*: Mato Grosso: Chapada; (USNM). Paraná: Castro; (USNM). Santa Catharina: near Concordia; Santa Catharina; (CM, USNM). Vague: "Brazil"; "Rio de Janeiro"; (CM, USNM). *Paraguay*: "Paraguay" (USNM). Sapucaí (near Villarrica) (USNM).

*Siproeta superba*

*S. s. superba* occurs in southern Mexico, Guatemala, and Honduras: the new subspecies *euoe* is found in the mountains of Costa Rica and western Panama.

This species is similar to the southern populations of *S. epaphus*, but is easily recognized by the presence of the second band of black-ringed blue spots crossing the forewing cell on the under side and by the male genitalia. The valve has the fold of the sacculus evenly curved, with no finger-like projection present, and the penis thickened, but instead of a few large projections around the middle, the penis bears a number of short sharp spines along much of its length.

*Siproeta superba superba* Bates

*Victorina superba* Bates, 1864: 141 (Guatemala).

*Victorina aphrodite* Butler, 1865: 483 (Mexico).

*Amphirene superba*, in part, Godman & Salvin, 1883 (1879-1901): 282.

The types of *V. aphrodite* Butler and *V. superba* G. & S. are in the British Museum (N.H.).

SPECIMENS EXAMINED (total 21 ♂): *Mexico*: Veracruz: Cordoba; Motzorongo; Veracruz; (USNM). Chiapas: 2 mi. west Palenque; (CM). *Guatemala*: "Guatemala" (CM, USNM). Alta Verapaz: Chejel; Quezaltenango: Volcán Santa María; (USNM). *Honduras*: "Honduras" (CM).





***Siproeta superba euoe*, new subspecies**  
(Plate V, figs. 1, 2)

*Amphirene superba*, in part, Godman & Salvin, 1883 (1879-1901): 282.  
*Victorina superba*, in part, of authors.

The *superba* populations of the mountains of Costa Rica and western Panama differ from those in the northern part of Central America, notably in the greater width and in the shape of the white band crossing both wings. In *S. s. superba* this band on the forewing has its distal edge nearly straight from the radial vein to the hind margin, but in *S. s. euoe* its outer edge is bowed outward so that the band is wider in  $M_3$ - $Cu_1$  than it is above or below that point. The band is wider at all points than in the northern subspecies, being at least 7 mm. wide at the subcostal vein of the hind wing, compared with only 6 mm. or less in *S. s. superba*. This absolute difference in width of the band is even more striking since the average size of members of the southern subspecies is a little smaller.

HOLOTYPE ♂: Avangarez, Costa Rica, July, W. Schaus; *ex* Schaus, C.M. Acc. 4960; det. "*Amphirene superba* Bates" by Schaus; genitalia slide No. 657, R. Fox, "ii-1949"<sup>2</sup>, C.M. Ent. type series no. 653.

PARATYPES: *Costa Rica*: San Mateo, 2♂ (USNM). *Panama*: Chiriqui, 2♂ (USNM).

*Siproeta stelenes*

*Siproeta stelenes*, the best known and commonest butterfly of the "*Victorina* complex," is distributed from one end of tropical America to the other. Its variability is attested by the two species names and six subspecies names that have been proposed for it in addition to one aberration and two quadrimorphs. The Linnean name *stelenes* has been almost universally misspelled as "*steneles*" for the past century. The uncritical presentation of Seitz (1914: 463) listed six supposed subspecies, in which the two quadrimorphs were given.

Our survey of the material available has led to the conclusion that there are four subspecies of *S. stelenes*. *Siproeta s. biplagiata* occurs in

<sup>2</sup>The slide bears the date "iv. 67", which is probably correct.—H.K.C.



PLATE V

Fig. 1. Upper side of *Siproeta superba euoe*, new subspecies. Holotype ♂. Avangarez, Costa Rica, July, *leg.* Schaus, CM Acc. 4960. Genitalia Slide No. 657 R. Fox II 49.

Fig. 2. Under side of same.



Central America from Mexico to Panama, and on Cuba.<sup>3</sup> The nominate subspecies is found on the rest of the Antilles from Jamaica and Hispaniola east and south, but not on Trinidad. The subspecies from Trinidad and all of tropical South America except western Ecuador is *S. s. meridionalis*. *S. s. sophene* occurs in Western Ecuador and Nariño, Colombia. All the other names associated with *stelenes* are either synonyms or not nomenclatorially available (aberration names or quadriminials).

The male genitalia of *stelenes* differ from those of other *Siproeta* primarily in the shape of the penis, which is quite large at its anterior end, then narrows and is fairly slender for its posterior two-thirds. It is armed at its midpoint with several rows of short, dark, bristle-like spines, and near its tip has some low projections. The valve is almost exactly like that of *epaphus*, with the down-turned projection, but its apex is a little more attenuated. The posterior double tip of the uncus is longer than in other species.

*Siproeta stelenes biplagiata* (Fruhstorfer)

*Victorina steneles biplagiata* Fruhstorfer, 1907: 13 (No locality cited).

*Victorina steneles biplagiata* forma "pallida" Fruhstorfer, 1907: 14 (Southern Mexico).

*Victorina steneles pallida* Seitz, 1914: 463.

*Victorina steneles* ab. "stygiaria" Schaus, 1913: 348 (Avangarez, Costa Rica).

*Victorina steneles insularis* Holland, 1916: 493 (Isle of Pines, Cuba).

No type was specified in the original description of *biplagiata*, nor was one mentioned by Martin (1922) in the list of the Fruhstorfer types. The Fruhstorfer collection, now in the British Museum (Natural History), includes some specimens bearing Fruhstorfer's determination as *biplagiata*. From among these we have selected a male [BM(NH), Rh 17076], from San Pedro Sula, Honduras, as the lectotype.

As a quadriminomial "*V. s. b. pallida*" was improperly proposed by Fruhstorfer, but the name was validated in 1914 when Seitz used it as a trinomial. The type of *pallida* Seitz is presumably the specimen Fruhstorfer designated as the type of his "pallida," although the *Inter-*

<sup>3</sup>West (1966, Ent. Rec. 78: 207) reports "*Metamorpha stelenes* L." from New Providence I., Bahamas. I have not seen the specimens and do not know which subspecies they represent.—H.K.C.

*national Code of Zoological Nomenclature* is silent on this point. Fruhstorfer stated, "Type von *pallida* aus S. Mexico," and this specimen (a female) was listed by Martin (1922).

[N.B. The specimen in the British Museum considered the lectotype bears these labels: "Mexico, Fruhstorfer;" "Steneles f. *pallida* Fruh." in manuscript; B. M. Type No. Rh 17074.—F.M.B.]

The specimen described as "*ab. stygiana*" by Schaus (1913) is in the U. S. National Museum.

Holland (1916: 493) did not select, either in his description or by labeling a specimen, a holotype for *V. steneles insularis*, and did not even record how many specimens from the Isles of Pines were in the series. From among 60 specimens in the syntypic series we hereby designate a male as lectotype.

[N.B. Fox had not selected and marked a lectotype for *insularis*. F.M.B. did so for him, choosing a male that seems to best represent the average appearance of the type series. The specimen designated carries these labels: (1) Nueva Gerona/Isle of Pines/G. Link Coll./vii.22.1912; and (2) Carn. Mus./Acc. 1745; (3) lectotype/Victorina/steneles/insularis/Holland/1916/—/F. M. Brown/xi.1968.—F.M.B. (Now C.M. Ent. type series no. 654)].

As given in our key above, *S. s. biplagiata* is the only subspecies with *two* greenish spots of nearly equal size in the discal cell of the forewing. In the other three subspecies the more distal of these two spots is absent on both sides of the wings, or occasionally it may be present but very minute. In general, specimens from Central America have the greenish median band wider than in specimens from Cuba, but some narrow-banded individuals occur in Central America and some wide-banded ones in Cuba. The Isle of Pines series in Carnegie Museum consists of specimens that are uniformly smaller than the average specimen from Cuba proper, and the median band tends to be narrow, as in *V. s. stelenes*. Such small, narrow-banded individuals also are found throughout the range of *biplagiata*.

SPECIMENS EXAMINED (total 242 ♂, 79 ♀): *Mexico*: Coahuila: Saltillo; (USNM). Sinaloa: Venadio (or Venodio?) (USNM). Tamaulipas: Tampico; (BM). San Luis Potosí: Valles; (USNM). Puebla: Orizaba. Veracruz: Attoyac; region of Córdoba; Córdoba (as Córdova); Jalapa; Motzorongo; Palo Gacho; (BM, USNM). Durango: nr. Durango. Guerrero: Acahuizotla (as Acaguizotla); "Buleas" [=Balsas?]; Dos Arroyos; Iguala; (BM, USNM). Oaxaca: Oaxaca; (BM). Chiapas: Escuintla; Finca El Real (between Ocosingo and Finca El Capulin); (CM). Yucatán: Pisté; Valladolid; (BM). Not located: Alto Mino; Campala; (CM, BM). Vague: "Mexico" (including types in BM reported to be those of *pallida*); "Rincón;" "Southern

Mexico;" (BM, CM, USNM). *Guatemala*: Yzabal (?): Motagua Valley; Baja Verapaz: Purulhá; San Jerónimo (as "Gerónimo"); Retalhuleu: Retalhuleu; San Sebastián; Department?: San Isidro (which?); (BM, USNM). Alta Verapaz-Yzabal: Polochic Valley (BM). "Guatemala" (CM). *British Honduras*: Corosal (Corozal?) (BM). *El Salvador*: Apopa; Lago de Coatepeque; Guazapa; Illopango; Lago de Ilopango (Apulo); Los Chorros (Santa Tecla); San Salvador; Santa Tecla; (BM, CM, USNM). *Honduras*: R. Choluteca (Cantarranus); Copán; San Pedro Sula; Tegucigalpa; Lago de Yojoa; (BM, CM, USNM). "Honduras;" (CM, USNM). *Nicaragua*: Chontales; Matagalpa; (BM). "Nicaragua" (BM). *Costa Rica*: Avangarez; Boruca; Buenos Aires; Esparta; Guápiles; Paraíso; Río Térraba (Puntarenas); Turrialba (Cartago); Turrucares (CM, F, USNM). Not Located: Santa Clara Valley (BM). "Costa Rica" (BM). *Panama*: Ancón; Balboa; Bugaba; Calobre; Las Cascadas; Chiriquí; Cocoli; Coco Solo; Corozal; David; Gatun; Río Hato; Tolé; (BM, CM, F, USNM). "Panamá, Panamá Canal Zone"; (CM, USNM). *Cuba*: Isle of Pines: Colombia; Nueva Gerona; (CM, USNM). Pinar del Río: Rangel; San Cristóbal; (BM, CM). Matanzas: Matanzas; (BM, USNM). Santa Clara; Santiago; (BM, USNM). Oriente: Guantánamo; Holguín; Sierra Maestra; Torquino Mass; Torquino River; (BM, CM). Not Located: Novojas; (USNM). "Cuba"; "St. Luis"; (BM, CM, USNM).

*Siproeta stelenes stelenes* (Linné)

*Papilio stelenes* Linné, 1758: 465 ("America," here restricted to Jamaica, W.I.).

*Metamorpha sthenele* Hübner, 1819 (1816-1826): 43.

*Victorina steneles* Blanchard, 1840: 447; pl. 14, fig. 1.

*Papilio lavinia* Fabricius, 1775: 450 ("America," here restricted to St. Croix, Virgin I., W.I.).

Past students who have dealt with *stelenes* have either ignored the questions of the holotype of the Linnean name and its type locality, or have found unacceptable solutions. Linné cited "Pet. gaz. t. 13, f. 1; Sloan. jam. 2. p. 217. t. 239. f. 9, 10.; Merian. Surin. s. t. 2." The first of these three references is to James Petiver's *GAZOPHYLACII NATURAE & ARTIS* (1702-1711); the second is to Sir Hans Sloane's *CATALOGUS PLANTARUM QUAE IN INSULA JAMAICA . . .* (1696); and the third to Countess Maria Sibylla Merian's *METAMORPHOSIS INSECTORUM SURINAMENSIVM . . .* (1705). The insect figured by Merian is *Philaethria dido* and the reference may be eliminated from further consideration. This simplifies the problem, since the insects figured by both Petiver and Sloane came from Jamaica and are now in the British Museum.

Whether to treat *sthenele* Hübner and *steneles* Blanchard as substitute names or revised spellings or as misspellings is a question of no im-



portance, though we favor the last view. What is important is that Blanchard's spelling reappeared in Kirby's authoritative *Catalogue* (1871), and then was repeated by nearly every author for the next seventy-five years.

For *Papilio lavinia*, Fabricius specified "Habitat in America. v. Rohr." The collection of Julius P. B. von Rohr was made in the West Indies, probably mostly on the island of St. Croix, and became part of Fabricius' own collection, which went to Kiel University, and now is on long-term loan to the Copenhagen Museum.

The distinctive feature of *Siproeta s. stelenes* is the narrowness of the greenish band on both sides, and of the postmedian spots on the upper side of the hind wing. The darker median band separating the two greenish series is especially wide, always wider than the postmedian elements, but not wider than the greenish submedian band. This same trend is exhibited on the forewing, and can be judged by the width of the greenish spot in Cu<sub>1</sub>-Cu<sub>2</sub>, which occupies only the basal half of the space.

SPECIMENS EXAMINED (total 216 ♂, 73 ♀): *Jamaica*: Accompong (St. Elizabeth); Annotto Bay; Bath; Buff Bay (Portland); Christiana; Constant Spring; Corn Puss Gap; Dolphin Head slopes; Enfield; Haining (Portland); Hamp (?); Hope Bay (Portland); John Crow Hill (St. Thomas); Millbank; Montego Bay; Morant Bay; Old Harbour; Portland Mountains; St. Andrew; St. Catherine; Trelawney (Belmore Castle, Pantrepant); (BM, CM, L, USNM). "*Jamaica*" (BM, CM, USNM). *Cayman* I.: Grand Cayman: west of Georgetown. *Haiti*: Arcahaie; Delmar; Kenscoff; Léogane; Morne Hôpital; Petionville; Port-au-Prince; Port de Paix; (BM, CM, L). "*Haiti*" (BM, CM, USNM). *Dominican Republic*: Santo Domingo; (BM). Not Located: Río Junta; (BM). *Puerto Rico*: Adjuntas; Aibonito; San Juan; Mayaguez; (CM, USNM). *Virgin Islands*: St. Croix (in part "Blossoms"); St. Johns; (CM, USNM). *Leeward Islands*: St. Kitts: Monkey Hill area; Old River Valley; (BM).

### *Siproeta stelenes meridionalis* (Fruhstorfer)

*Victorina steneles meridionalis* Fruhstorfer, 1909: 41 (Rio Grande do Sul).

*Victorina steneles steneles* forma "bipunctata" Fruhstorfer, 1907: 14 (Espírito Santo, and Rio Grande do Sul, Brazil).

*Victorina steneles bipunctata* Seitz, 1914: 463.

*Victorina steneles didoides* Fiedler, 1931: 501 (Peru).

*Victorina steneles vilarsi* Bryk, 1953: 95 (Taracua, Rio Uaupes, Brazil).

The type of *V. s. meridionalis* is in the British Museum (Nat. Hist.), number Rh. 17073. Fruhstorfer described "bipunctata" as a quadri-



nomial, but the name was legalized when Seitz used it as a trinomial; the type is in the British Museum (Nat. Hist.), number Rh 17072. We have not located the type of *didoides* Fiedler. The type of *vilarsi* Bryk is in the Stockholm Museum. Both are synonyms.

The principal South American form is characterized by the wide greenish band and the large greenish postmedian spots. It occurs throughout the tropical parts of the continent except in western Ecuador and southwestern Colombia (where it is replaced by ssp. *sophene*) and is surprisingly variable.

**SPECIMENS EXAMINED** (total 165 ♂, 41 ♀): *Trinidad*: Carenage; Cascade Mountain Road (St. Ann's Parish); Hololo Mountain Road (St. Ann's Parish); Port of Spain; Tacarigua; (CM, L, USNM). Not Located: "Bamboo Paige"; (CM). "Trinidad" (BM, CM, L). *French Guiana*: "French Guiana" (BM). *Surinam*: Paramaribo; (L). *British Guiana*: Kaiteur Falls; Kartabo; Rockstone (Essequibo); (BM, CM, USNM). Not Located: Mackenzie; (L). "British Guiana" (BM). *Venezuela*: Carabobo: Puerto Cabello (as Porto Cabello); San Esteban (as San Estevan, Puerto Cabello); (BM, CM). Dist. Federal: Puerto la Cruz; (CM). Miranda: Naiguatá Mt.; Santa Lucia; (CM). *Colombia*: Magdalena: Aracataca; Bonda; Cacagualito; Don Diego; Manaure; Minca; (BM, CM). Cundinamarca: Bogotá; "de Bogotá a Buenavista"; (BM, CM, USNM). Caldas: Pereira; (BM). Cauca: Las Juntas (as Juntas); (BM). Metá: Tolima (El Santario). Not Located: San Vicente; "Colombia," "Interior of Colombia"; (BM, CM). *Ecuador*: Tungurahua: La Merced (on Río Pastaza below Baños); (CM). Oriente: Canelos; (BM). "Ecuador" (BM). *Peru*: Amazonas: San Pedro; (CM). Loreto: Iquitos; Yarina-Cocha; (CM). Huánuco: Pozuzo (as Pozuzo); (BM). Cuzco: Río Chanchosmayo (as Chanchamayo); (BM, USNM). Not Located: "La Pampa" (Río Tavera), "Yakuamuyo"; (CM, L). "Peru" (CM). *Bolivia*: La Paz: Apolobamba; (BM). Santa Cruz: Buenavista; Portachuelo (Río Palmetillos); Prov. del Sará; Río Surutu; Río Yapacani; (CM). "Bolivia, east slope of Andes (Chapare)"; (BM). *Brazil*: Amazonas: Arimã (Río Purús); Nova Olinda (Río Purús); São Paulo de Olivença; (BM, CM). Pará: Obidos; Santarem; (BM, CM). Mato Grosso: Chapada (in part as Chapanda); Cuyabá; (BM, CM, USNM). Goiás: Goyaz (as Goyez, Pujol?); Espírito Santo; (BM). Minas Geraes: Sete Lagoas; (CM). Rio de Janeiro: Santo Antonio de Brotos (District São Fidelis); (BM). Guanabara: Novo Friburgo (as Nova Friburgho); Rio de Janeiro; (BM, CM). São Paulo: Bauru; (CM). "Amazonas" (BM). Paraná: Castro; Iguarassú; (BM, USNM). Not Located: Tarapote. Vague: "Brazil"; "Brasilla"; "Lower Rio Madeira"; "Rio Grande do Sul" (including types of *meridionalis*); "Santarem" (Amazonas); (CM). *Paraguay*: Villarrica (as Villa Rica); (CM). "Paraguay" (BM). *Argentina*: Salta: Río Bermejo; (CM). Santa Fé: Villa Ana; (BM). "N. Argentina"; "Guayaquil"<sup>4</sup>; (BM).

<sup>4</sup>Presumably Ecuador, but probably erroneous.

*Siproeta stelenes sophene* (Fruhstorfer)

*Victorina steneles sophene* Fruhstorfer, 1907: 14 (Pacific coast, Ecuador).

The type bears number Rh 17071 in the British Museum (Natural History).

This is the only subspecies other than *S. s. meridionalis* found in continental South America. The greenish submedian band is narrower than the dark median band. Although the greenish post-median spots of the hind wing are as narrow as in *stelenes*, they are placed so that they are narrower than the submarginal band of darker color beyond them.

SPECIMENS EXAMINED (total 26 ♂, 8 ♀): *Ecuador*: Pichincha: Santa Domingo de los Colorados (Río Baba, Hacienda "El Rosario," Hacienda "San Jose," Río Toachi); (CM). Bolívar: Balzapamba (as Balzabamba) (CM). Guayas: Guayaquil; Narantal; La Puntilla; El Triunfo; (CM, USNM). Chimborazo: Chimbo; Dos Puentes; Huigra; (BM, CM). El Oro: El Oro, 4 ♂ (CM). "Ecuador" (including type of *sophene*) (BM, USNM).

Genus *Metamorpha* Hübner, 1819

*Metamorpha* Hübner, [1819] (1816-1826): 43. Type species, *Papilio elissa* Hübner [1819], designated by Scudder, 1875.

*Victorina*, in part, of authors.

The generic name *Metamorpha* has been incorrectly used in the past for *Philaethria dido*, following Godman & Salvin, who emphasized in a footnote [1883 (1879-1901): 280] that, "We use Hübner's name *Metamorpha* in a different sense from Dr. Aurivillius. Our application of it dates from December 1881 (*antea*, p. 166), that of Dr. Aurivillius from the following year [cf. Aurivillius 1882]." The *International Code of Zoological Nomenclature* (1964 edition) does not accept such priority of usage, an aspect of the once generally followed "Rule of the First Revisor." Kirby [1894 (1894-1912)] attempted to legalize the Godman & Salvin use of *Metamorpha* by designating *P. dido* as a type species, but Scudder (1875) had already taken care of the matter by designating *P. elissa*. Stichel (1907) reviewed the whole situation and used *Metamorpha* correctly, but Seitz (1914) ignored Stichel.

*Metamorpha elissa* Hübner

There are two subspecies. *M. e. elissa* is found from Colombia to Peru, and throughout the Amazon valley. *M. e. pulsitia* occurs in eastern Bolivia.

*Metamorpha elissa elissa* Hübner

*Metamorpha elissa* Hübner, 1819 (1816-1826): 43, as a replacement name for *P. sulphitia* Stoll, [1780].

*Papilio sulphitia* Stoll, [1780], in Cramer, 1775-1791: 4:77; pl. 328, figs. A, B (Surinam). Junior homonym of *P. sulphitia* Cramer, 1779 (1775-1791): 3; pl. 214, figs. E, F (An oriental insect).

*Nymphalis symachia* Godart, 1821: 379, as a replacement name for *P. sulphitia* Stoll, [1780].

As replacement names, *M. elissa* and *N. symachia* both take as their types the type of the name replaced, *P. sulphitia* Stoll. This type was in the Cramer collection, most of which has been lost, but some Cramer specimens went to the British Museum (N.H.) *via* the Rothschild collection *via* the Felder collection *via* the van Eyndhoven collection. The type of *P. sulphitia* evidently was not one of those and has been lost. In order to insure correct usage of the name, we designate as neotype. . . .

[N.B. There is a lacuna in the manuscript at this point. I searched the Carnegie Museum collections for any Surinam material that might be used for the required neotype. There is none. I wrote T. G. Howarth at the British Museum (N.H.) and asked him to select a specimen from Surinam that conforms with Stoll's figure (*l.c.*). We both were surprised that no undoubted Surinam or Guiana specimen is among their large collections. I extended the search to other museums. No one could supply me with undoubted Surinam specimens of *elissa*. I lack the knowledge necessary to suggest from where Cramer or Stoll had received the model for the figure of *sulphitia* in Volume 4 of their work. Therefore I have decided that in spite of great need for a neotype for the name *Papilio sulphitia* Stoll [1780], its designation had best be made by a future student of the sources of material used by Cramer and Stoll.—F.M.B.]

The white median band on the upper side of the forewing is about the width of the dark band beyond it, and on the under side of both wings all the markings are sharp and clean-cut.

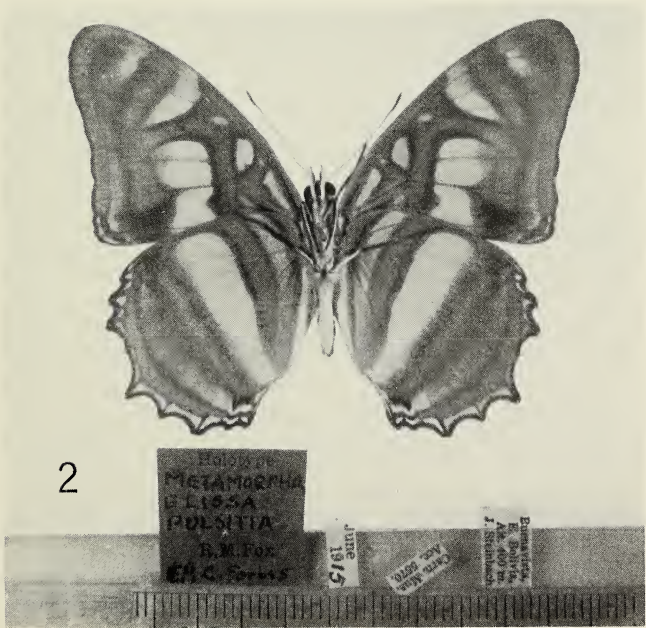
SPECIMENS EXAMINED (total 112 ♂, 19 ♀): *Colombia*: Antioquia: head of Río Carare; (USNM). Cundinamarca: Bogotá; Melgar; Muzo; (BM, CM, USNM). Metá: Tolima (El Santario); Villavicencio; (BM). "Colombia"; "Environs of Bogotá"; "Interior of Colombia"; "Río Magdalena à Bogotá"; (BM, CM, L, USNM). *Ecuador*: Tungurahua: Hacienda "La Mascota" (Río Topo); Río Topo; (CM).

## PLATE VI

Fig. 1. Upper side of *Metamorpha elissa pulsitia*, new subspecies. Holotype ♂. Buenavista, E. Bolivia, Alt. 400 m., leg. J. Steinbach, June 1915. CM Acc. 5570.

Fig. 2. Under side of same.







Oriente: Aguano; Canelos (Río Bobonaza); Cururai; Zamora; (BM). "east Ecuador"; "Ecuador, Pacific slope"; (BM, USNM). *Peru*: Amazonas: Chachapoyas; San Pedro; (BM, CM). Loreto: Charapa; Río Napo; Ucayali; (BM, CM). San Martín: Moyabamba; (BM). Huánuco: Pozuzo (as Puzuzo); Junín: Satipo; (CM). Cuzco: Río Chanchosmayo (as Chanchamayo); (BM, USNM). Not Located: "La Pampa" (Río Távora); (CM). "Peru"; "Southeast Peru"; (BM, CM). *Bolivia*: "Central Bolivia"; (BM). *Brazil*: Amazonas: Bôca do Acre (Río Purús); Ega; Hyutanahan (Río Manicoré Dist., Santa María and Santa Caterina de Marmelos—Río Madeira located as Santa María dos Marmelos); São Paulo de Olivença, Upper Amazon; (BM, CM). "Amazon"; "Río Napo"; "South America"; (BM, USNM).

### *Metamorpha elissa pulsitia*, new subspecies

Plate VI, figs. 1, 2

All specimens that we have seen from eastern Bolivia differ consistently from nominate *M. e. elissa* as follows:

The white median band on the upper side of the forewing is much narrower than the band of dark coloring between it and the margin, but in *elissa* these two bands are of about the same width. On the under side of both wings all dark markings are dilute and smudged, not cleanly drawn and clear. On the under side of the forewing there is a silvery white band between the dark marginal line and black-brown edging the outer side of the orange post-median band in the nominate subspecies, but in *pulsitia* this silvery white coloring is limited at most to small areas near the apex and anal angle, or may be entirely absent.

HOLOTYPE ♂: Buenavista, Santa Cruz, Bolivia, 400 m.; June 1915, J. Steinbach; Carnegie Museum Acc. 5570.

ALLOTYPE ♂: Río Surutú, E. Bolivia, 350 m.; April 1915, J. Steinbach; Carnegie Museum Acc. 5570. Right wings mounted on slide No. 26, forelegs No. 27.

PARATYPES, 57 ♂, 18 ♀: all in Santa Cruz, Bolivia: Buena Vista 400 m.; Río Surutú, 300 m.; Prov. del Sará, 450 m.; Río Yapacani, 600 m.; Portachuelo, Río Palmetillas; Sta Cruz de la Sierra. All were collected by José Steinbach, and all are in CM. C.M. Ent. type series no. 655. *Peru*: No specific locality, 1 ♂ (USNM).

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# THE WELSH CAVE PECCARIES (*PLATYGONUS*) AND ASSOCIATED FAUNA, KENTUCKY PLEISTOCENE

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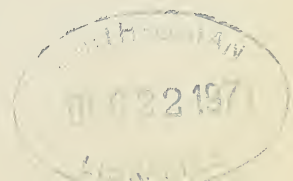
## INTRODUCTION

Welsh Cave was discovered in 1965 by a group of Kentucky cavers: Martin Traugott, William Andrews, Michael Hornback, and Raymond McAdams. It was reported to Dr. Thomas Barr, University of Kentucky, who informed A. D. McCrady of the possibility of a Pleistocene bone deposit on the evidence of a peccary skull that the discoverers had picked up in the cave. Carnegie Museum fieldwork at the site was carried out: Thanksgiving weekend, 1965; the weekend of May 14, 1966; September 9-16, 1966; and September 7-15, 1967, a total of 19 days. The excavated area measured approximately 10 feet long, two to three feet wide, and six feet to less than one foot deep. Approximately one-half ton of matrix was removed for washing and removal of microfauna. Pollen analysis by the Laboratory of Paleo-environmental Studies, University of Arizona, proved negative. At present, access to the cave is denied us, and we can only stress the preliminary nature of this report.

## ACKNOWLEDGMENTS

In addition to those mentioned above who discovered the site and were alert enough to realize its potential scientific value, we would like to thank Mr. and Mrs. Welsh, former owners of Welsh Cave; and James Huff and George Jewell, local residents. Field assistance, without which this paper would not have been possible, was provided by Janet Bailey, Rita Hamilton, Marilyn McCrady, Ann Rhunka, Charles Schwab, and

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Jodi Watts (figs. 3, 8); laboratory assistance by A. Lee Ambrose, Dr. Elaine Anderson, Galen Barton (figs. 9, 10), Carla H. Beck (figs. 18, 19, 22-25, 29, 30), Eleanor (Adam) Gossen, Alice Guilday (figs. 26, 27, 31), Helen McGinnis, and Donald Tanner (figs. 11-17). We would also like to thank Dr. Roger Barbour, Dr. Craig Black, Dr. Mary Dawson, Dr. J. Kenneth Douth, Caroline Heppenstall, Dr. Barbara Lawrence, Dr. Ernest Lundelius, Dr. M. Graham Netting, Dr. Paul W. Parmalee, Bob Slaughter, and Dr. Frank Whitmore for encouragement and assistance. Pollen analysis was provided by Dr. Peter Mehringer and Dr. Paul S. Martin, University of Arizona. Measurements of *Platygonus compressus* from University of Cincinnati collections (Reading, Ohio), were obtained through the courtesy of Mrs. Elizabeth Dalvé.

We also wish to thank Dr. Richard Van Gelder of the American Museum of Natural History for permission to section the skull of a white-lipped peccary, and for the loan of specimens; Mr. Terrence Coffin-Grey, National Museum, Rhodesia, for providing us with the skull of a recent wart hog; and Dr. Lyle K. Sowls, Arizona Cooperative Wildlife Research Unit, for the donation of a collared peccary for dissection.

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### CAVE DATA

#### LOCATION

Welsh Cave, named for a previous landowner, is located in central Kentucky (map, fig. 31) in the southern portion of the Blue Grass region immediately west of the Cumberland Plateau on the east side of the Kentucky River, about 100 miles southeast of the junction of the Kentucky and Ohio rivers. It is in Woodford County, about 3½ miles southwest of Troy, approximately halfway between Nonesuch and Mundy's Landing, at longitude 84° 44' 50" W., latitude 37° 52' 25" N. Its elevation is 880 feet, Wilmore Quad. US.G.S. 7.5' series, or Winchester sheet WJ 16-9, 1:250,000 scale. Detailed road directions are on file at Carnegie Museum, Section of Vertebrate Fossils.

#### LOCAL GEOGRAPHY

This area of Kentucky, lying as it does to the west of the precipitous Appalachian Mountain country and the broken hills of the Cumberland Plateau, is gently rolling farmland of relatively little relief. It is a typical karst area with numerous caves and sinkholes, into which the widely meandering Kentucky River has incised itself 300 to 400 feet. The aver-

age elevation varies from 800 to 900 feet. Formerly covered with a dense oak-hickory forest, the land is now about 80% cultivated. Those wooded areas that remain are woodlots, hedgerows, and stream borders. The region is typical of the eastern Carolinian biotic province (Dice, 1943). Trees noted in the immediate vicinity include *Quercus* (oak), *Ulmus* (elm), *Carya* (hickory), *Platanus* (sycamore), *Sassafras* (sassafras), *Fraxinus* (ash), *Juniperus* (cedar), and either *Gleditsia* or *Robinia* (locust). Prickly pear cactus (*Opuntia*) is common in the poor, well-drained limestone soil.

#### DESCRIPTION OF CAVE

Welsh Cave is small and relatively featureless. The entrance is on the side of a large, shallow, circular depression in the surface of the ground, approximately 100 feet in diameter and 10 feet deep (fig. 1) with a gently sloping perimeter. The depression is even-floored, grassed over, and forms part of the local pasture. The surrounding area does not have



Fig. 1. From the east rim looking toward the west rim of the collapsed sink containing Welsh Cave, Woodford County, Kentucky. Cave entrance between automobile and right-hand figures.



enough elevation to provide the quantity of surface-derived material that would have been required to fill a depression of such dimensions if originally it was an open cenote of any great depth. The sink was probably formed by direct collapse of a former cave system of which only the small passage, the present Welsh Cave, survives. The present entrance is on the west rim of the collapsed areas (fig. 2), and one must crawl over breakdown and talus, almost brushing the ceiling of the passageway, to get into the cave. The passage beyond the entrance is the remnant of a ceiling slot (map, fig. 3), i.e., the upper portion of a joint-controlled cave passage, greatly constricted. It was not the entrance by which the Pleistocene component of the deposit entered. The cave apparently collapsed further after the bulk of the faunal remains accumulated, leaving only the ceiling slot, a passageway just large enough



Fig. 2. Present surface entrance of Welsh Cave, Woodford County, Kentucky, partially obscured by rock pile. West rim of collapsed sink in background.

Fig. 3. Map of Welsh Cave, Woodford County, Kentucky.

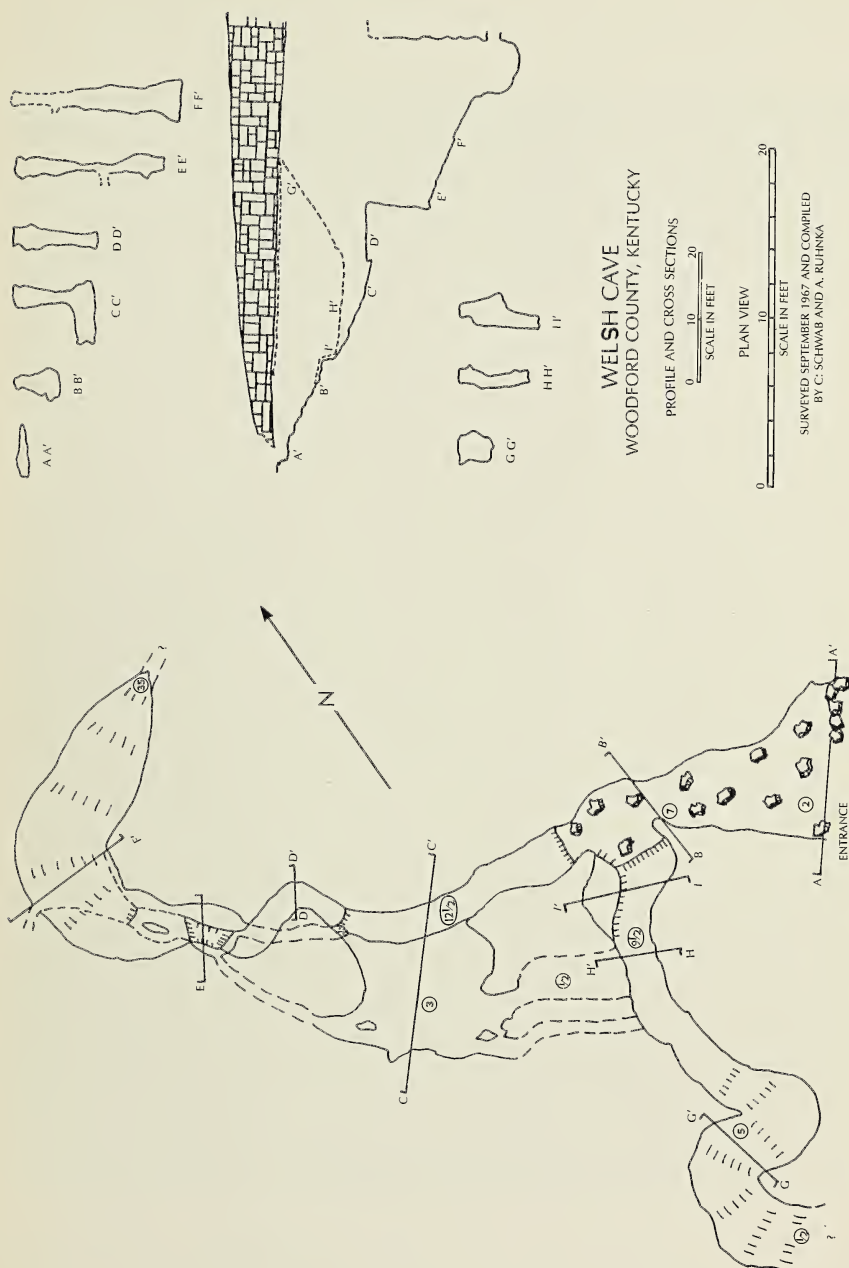






Fig. 4. Welsh Cave, Woodford County, Kentucky. Figure facing west, excavating floor of Oval Room. Remnants of "natural bridge" above feet of excavator. "Drainage slot" center background.



Fig. 5. "Drainage slot," northeast end of Oval Room, Welsh Cave, Woodford County, Kentucky. Peccary skull found exposed on foreground talus.



for a normal-sized human being. This slot winds along to the northwest approximately 40 feet, its floor descending at an angle of about  $45^\circ$ , its width no more than several feet. At this point one arrives at a miniature dome-pit about three to four feet in diameter, which drops into an oval-shaped room (fig. 4) about 10 feet long and three to four feet wide, trending in a northeasterly direction and terminating in a narrow crack that appears to be the drain for the entire cave during periods of high precipitation (fig. 5). The floor level of the Oval Room drops about five feet as one approaches the end of the cave. It was on the talus of this room that a complete skull of the peccary *Platygonus compressus* was found by the discoverers of the cave. Before excavation the Oval Room was floored by ceiling breakdown, humus, animal droppings, bones (some, e.g., opossum (*Didelphis marsupialis*), were obviously of Recent origin), clay, and even a sewing thimble. The material did not appear to be water-sorted, but a typical talus pile, gravity-accumulated. The matrix at this point was heterogeneous in age, composed of both Pleistocene and Recent materials derived from the present entrance during periods of heavy surface runoff. It became apparent upon excavation, however, that only the superficial portion of the deposit was contaminated by modern surface-derived materials and that it did possess some stratigraphic integrity that became more apparent as excavation proceeded. Evidence of secondary deposition became scarcer, and it is probable that all species represented were contemporaneous. Opossum, for instance, was not represented in the excavation proper, but was found in the surface talus, as was extraneous material like bits of glass and the thimble. One broken atlatl weight (fig. 6), was discovered directly beneath the skull in association with skeletal material of an extinct peccary near the bottom of the stream passage and well within what we consider late Pleistocene strata. It may, however, have been secondarily deposited. From its style, it dates to the Late Archaic period, approximately 3,000 B.C., according to Dr. Don Dragoo, Section of Man, Carnegie Museum, approximately 10,000 years later than the collagen-derived carbon-14 date of the associated peccary bones. Notwithstanding these few items, obviously of later age, the fauna seems to be primarily late Pleistocene.

Excavation of the deposit began at the extreme northeast end of the Oval Room, at the drainage slot (see position of figure in fig. 5 facing up-talus), and proceeded northwest, biting into the Oval Room talus. The floor of the excavation was approximately that of the local water

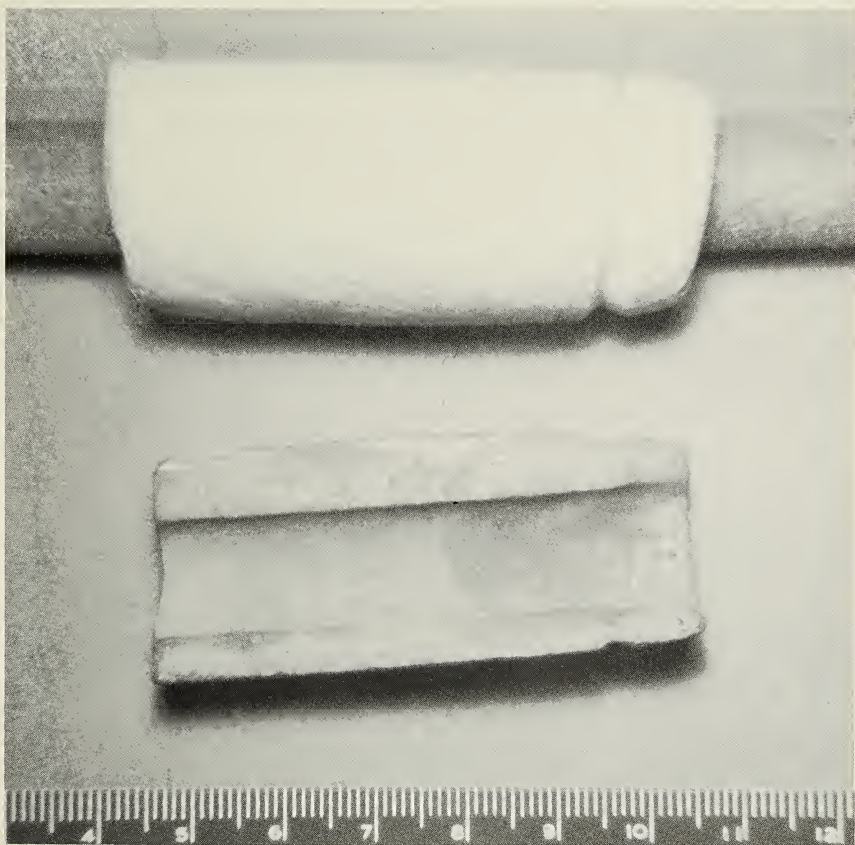


Fig. 6. Broken atlatl, or spear-throwing weight, from Welsh Cave, Woodford County, Kentucky. Scale in millimeters. Top: external view, plaster cast. Bottom: internal view, original specimen. Atlatl weight had split in half longitudinally before deposition and all edges showed signs of tumble abrasion.

table, and the matrix was unctuous mud, saturated with water. As excavation proceeded in the up-talus direction it became apparent that the Pleistocene-bearing strata continued under a natural bridge of limestone at foot 3 (foot 0 at drainage slot). Excavation was continued under this limestone ledge for an additional three feet. The level of the water table was only 15 inches below tunnel ceiling, and recovery methods other than muck dredging were impossible. Peccary bones were abundant at feet 4 and 5, and included post-cranial material as well as complete skulls. Excavation continued beyond foot 6, at which point the



ceiling rose rapidly from 15 inches to almost 5 feet. The natural bridge was removed by dynamiting. Its former site may be seen in the mid-ground of figure 4. The excavator is lying at about water level. The excavating face at the termination of Carnegie Museum fieldwork measured about four to five feet wide and five to six feet high (fig. 7). Stratigraphy was not clear-cut but was revealed in varying shades of color and texture (fig. 8). The cave passage appeared to have been originally filled with sterile, light-brown to gray, to yellow fine-grained clay, with no obvious stratification, which had subsequently been deeply channeled along the walls of the cave passage. These channels were filled with darker bone-bearing clays, coarse cave breakdown, and talus rock. Most of the bone material was found against the northwestern wall, but some was found throughout the passageway except in the center core. There is no evidence of sustained water-sorting, and most of the



Fig. 7. Excavating face, west end of Oval Room, Welsh Cave, Woodford County, Kentucky, after removal of "natural bridge" illustrated in midground of fig. 4. Fossil bones recovered from the matrix wall directly behind excavator.

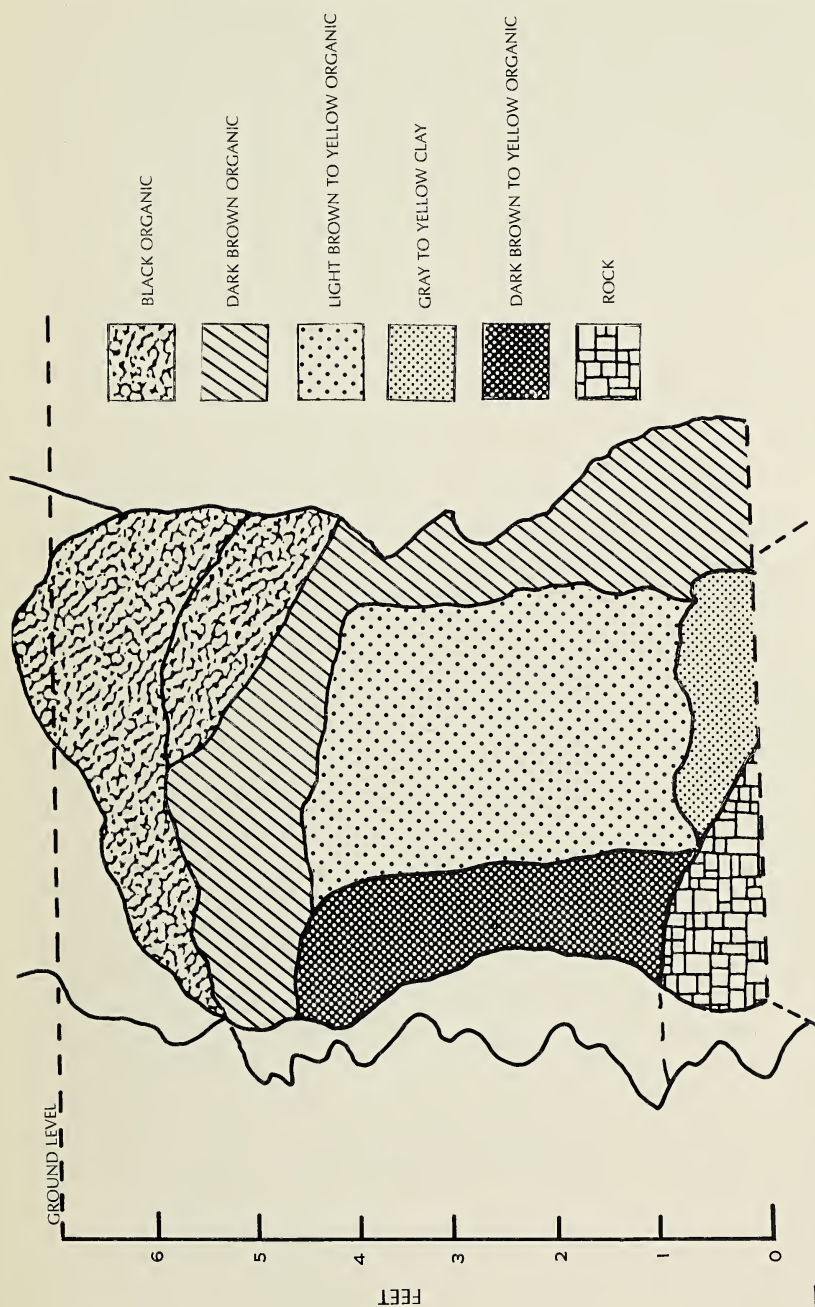


Fig. 8. Diagram of excavating face shown in fig. 7. Further explanation in text.

materials appear to have been laid down by relatively still water deposition. All skeletons were found disarticulated and scattered, occasionally badly mutilated and crushed by talus blocks, indicating some degree of post-depositional churning. Some of the bones and the atlatl weight were tumbleground, although not excessively so. At this point excavations were unexpectedly and precipitously terminated by a change in ownership of the cave. The size of the remaining bone deposit is unknown, but it is probably extensive.

In general all bones were in good condition. Degree of preservation varied from excellent (unworn, uncrushed) to poor (crushed by talus blocks, ground in some instances into paste). In this compact jumble of peccary remains, representing at least 31 individuals, only one instance of articulation, adjoining thoracic vertebrae, was noted. Bone color varied from light ivory to black, and mineralization appeared to be at a minimum, although there were traces of iron or manganese blooms penetrating the bone structure. Although most bone showed little sign of erosion, the almost universal disarticulation, the finding of isolated teeth, and conversely, skulls and mandibles minus teeth, and some evidence of tumble-polishing showed that at least a portion of the bones had been water-washed. Large skulls and major limb elements occurred, intermingled with sesamoids, and carpal, tarsal, and hyoid elements. Skulls of mouse and shrew-sized animals, while not common, were well preserved. The bulk of the collection was probably built up by animal remains tumbling down former talus slopes to repose against the walls of the cave.

#### CARBON-14 DATE

Fragmentary ribs and limb bones of the commonest large mammal in the deposit, the extinct flat-headed peccary (*Platygonus compressus* LeConte) were submitted to Isotopes, Inc., for dating. A date of 12,950  $\pm$  550 years B.P. (I-2982) was derived from the collagen content of the bones. It is assumed that this date applies to the majority of the specimens recovered from the fauna.

#### ABBREVIATIONS

C = Canine  
P = Premolar

M = Molar  
d = Deciduous tooth  
I = Incisor

CMSC = Central Missouri  
State College

DC = Carnegie Museum Section  
of Mammals Donor  
Catalog



$\frac{1\ 2\ 3}{1\ 2\ 3}$  = Tooth position  
and number

B.P. = Before Present

$\bar{X}$  = Mean

O.R. = Observed range

V = Coefficient of variation

N = Sample size

S.D. = Standard deviation

CM = Carnegie Museum

AMNH = American Museum of  
Natural History

G = Guilday field number

I = Isotopes, Inc.

M = University of Michigan  
C-14 sample number

MCZ = Museum of Comparative  
Zoology (Harvard  
University)

SIU = Southern Illinois  
University

TMM = Texas Memorial Museum

NMNH = National Museum of  
Natural History

The following sites are referred to repeatedly throughout the text. References to primary articles dealing with these sites are given here:

New Paris No. 4, Pennsylvania—Guilday, Martin, & McCrady, 1964

Bootlegger Sink, Pennsylvania—Guilday, Hamilton, & McCrady, 1966

Robinson Cave, Tennessee—Guilday, Hamilton, & McCrady, 1969

Crankshaft Pit, Missouri—Parmalee, Oesch, & Guilday, 1969

Meyer Cave, Illinois—Parmalee, 1967

Cumberland Cave, Maryland—Gidley & Gazin, 1938

Natural Chimneys, Virginia—Guilday, 1962



TABLE 1. WELSH CAVE LOCAL FAUNA

Species	Minimum Number of Animals	Minimum Based on:	Number of Cataloged Specimens	Carnegie Museum Catalog Number
Class MAMMALIA Linnaeus, 1758				
Order INSECTIVORA Bowdich, 1821				
Family: Soricidae Gray, 1821				
<i>Sorex palustris</i> Richardson *x				
water shrew	2	mandibles	4	20006
<i>Microsorex hoyi</i> (Baird) *x?				
pygmy shrew	2	mandibles	4	20005, 20147-9
<i>Blarina brevicauda</i> (Say) *				
short-tailed shrew	2	mandibles	3	20144-5
Family: Talpidae Gray, 1825				
<i>Scalopus aquaticus</i> cf. <i>machrinus</i> (Rafinesque) *				
eastern mole	1	humerus	2	12920
Order CHIROPTERA Blumenbach, 1779				
Family: Vespertilionidae Gray, 1821				
<i>Myotis</i> Kaup, ?species *				
little brown bat	2	mandibles	2	20150
<i>Pipistrellus</i> cf. <i>subflavus</i> (F. Cuvier) *				
pipistrelle bat	1	mandible	1	20151
Order LAGOMORPHA Brandt, 1855				
Family: Leporidae Gray, 1821				
<i>Sylvilagus</i> Gray, ?species				
cottontail rabbit	1	mandible	6	12964
<i>Lepus</i> cf. <i>americanus</i> Erxleben *x				
snowshoe hare	1	humerus	4	20202
Order RODENTIA Bowdich, 1821				
Family: Sciuridae Gray, 1821				
<i>Spermophilus tridecemlineatus</i> (Mitchill) *x				
thirteen-lined ground squirrel	43	mandibles	118+	12627, 12890-12913, 12963, 20014-5, 20155-83
cf. <i>Tamiasciurus hudsonicus</i> (Erxleben) *x				
red squirrel	1	incisor	1	20153

\* = Species discussion in text.

# = Extinct.

x = No longer living in the site area.

TABLE 1. WELSH CAVE LOCAL FAUNA (continued)

Species	Minimum Number of Animals	Minimum Based on:	Number of Cataloged Specimens	Carnegie Museum Catalog Number
Family: Geomyidae Gill, 1872				
<i>Geomys</i> cf. <i>bursarius</i> (Shaw) *x plains pocket gopher	3	mandibles	16	12918, 12962, 20152
Family: Cricetidae Rochebrune, 1883				
<i>Peromyscus</i> Gloger, ?species white-footed mouse	2	maxillae	3	12916, 20184-5
<i>Clethrionomys</i> cf. <i>gapperi</i> (Vigors) *x red-backed vole	1	M <sup>2</sup>	1	20008
<i>Phenacomys</i> cf. <i>intermedius</i> Merriam *x spruce vole	1	M <sup>1</sup>	1	20007
<i>Microtus</i> cf. <i>pennsylvanicus</i> (Ord) * meadow vole	11	mandibles	21	12917, 20010, 20012, 20188-92
<i>Microtus xanthognathus</i> (Leach) *x yellow-cheeked vole	2	skulls	6	12914-5, 20011, 20186-7
<i>Pitymys</i> McMurtrie (or <i>Pedomys</i> Baird) * pine (or prairie) vole	13	M <sub>1</sub> 's	24	20009, 20013, 20193-7
Family: Erethizontidae Thomas, 1897				
<i>Erethizon dorsatum</i> (Linnaeus) *x porcupine	2	skulls	23	12654, 20199-20201
Order CARNIVORA Bowdich, 1821				
Family: Canidae Gray, 1821				
<i>Canis dirus</i> Leidy * # dire wolf	2	skull, mandible	12	12625
Family: Ursidae Gray, 1825				
<i>Ursus arctos horribilis</i> Ord *x grizzly bear	2	teeth	6	12617

\* = Species discussion in text.

# = Extinct.

x = No longer living in the site area.

TABLE 1. WELSH CAVE LOCAL FAUNA (continued)

Species	Minimum Number of Animals	Minimum Based on:	Number of Cataloged Specimens	Carnegie Museum Catalog Number
Family: Mustelidae Swainson, 1835				
<i>Mustela nivalis</i> Linnaeus x least weasel	1	skull	2	12919, 20203
<i>Taxidea taxus</i> (Schreber) *x badger	1	temporal bone	1	12640
Order PROBOSCIDEA Illiger, 1811				
Family: Elephantidae Gray, 1821				
<i>Mammuthus</i> Burnett, ?species * # mammoth	1	partial tooth	12	12628
Order PERISSODACTYLA Owen, 1848				
Family: Equidae Gray, 1821				
<i>Equus</i> Linnaeus, ?species * # horse	1	second phalanx	1	12629
Order ARTIODACTYLA Owen, 1848				
Family: Tayassuidae Palmer, 1897				
<i>Platygonus compressus</i> LeConte * # flat-headed peccary	31	mandibles	1,183	12624, 12630-39, 12641-53, 12656-7, 12684, 12885-9, 12921-60, 20113-41

\* = Species discussion in text.

# = Extinct.

x = No longer living in the site area.

## SPECIES NOTES

## Talpidae

*Scalopus aquaticus* cf. *machrinus* (Rafinesque)—Eastern mole

MATERIAL: CM 12920. 1 partial humerus; 1 molar.

REMARKS: The contemporaneity of burrowers like moles with a cave deposit is always suspect, and *Scalopus* may or may not date from *Platygonus* times. Unfortunately, the humerus was too fragmentary to measure, but it appears to fall within the size range of the resident sub-

species, *S. a. machrinus* (Rafinesque). Although this subspecies is characterized by its great relative size, it "... retains its characters with remarkable regularity throughout its range. Specimens from the Mississippi Basin in upper Wisconsin . . . are as large as specimens from the type region [Lexington, Ky.], if not slightly larger." (Jackson, 1915: 44.) Size, therefore, at least within the geographic area we are interested in, is no indication of possible living population equivalents in *Scalopus* as it is in forms where Bergmann's Response is pronounced, as in *Blarina brevicauda*.

### Soricidae

#### *Sorex palustris* Richardson—Water Shrew

MATERIAL: CM 20006. 2 left, 1 right, mandibles with partial dentitions; right maxilla with P<sup>3</sup>-M<sup>2</sup>.

REMARKS: This is the first record of the water shrew from Kentucky. Although it is found on the summits of the higher Appalachian Mountains to the east, it occurs no farther south in the American Midlands than central Wisconsin and Minnesota. It is also known from at least the following late Pleistocene Midland periglacial localities: Crankshaft Pit, Missouri; Robinson Cave, Tennessee. Measurements are: length of dentary, 10.1 mm; C-M<sub>3</sub>—5.3 mm; M<sub>1</sub>-M<sub>3</sub>—3.7 mm., 4.3 mm.

#### *Microsorex hoyi* (Baird)—Pigmy shrew

MATERIAL: CM 20005, 20147-20149. 2 right mandibles, 1 anterior half of skull, 1 maxilla fragment.

REMARKS: This is apparently the second record of *Microsorex* from Kentucky (Barbour, 1956). It is common in many late Pleistocene periglacial cave deposits. At least 17 individuals were recovered from Robinson Cave, Tennessee, 110 miles south of Welsh Cave. Measurements are: Length of dentary—6.3 mm; height of ascending ramus—2.9 mm; M<sub>1</sub>-M<sub>3</sub>—2.8 mm.

#### *Blarina brevicauda* (Say)—Short-tailed shrew

MATERIAL: CM 20144-5. 1 right mandible, full dentition; 1 mandible fragment, no teeth; 1 isolated lower incisor.

REMARKS: No definitive statement can be made from so small a sample. However, the two jaws are so dissimilar in size that one may derive from the smaller race *B. b. kirtlandi*, now found in the area. The other may represent more northern racial stock, as was the case at Meyer Cave, Illinois. Compare the measurements of the larger specimen (CM 20144) with samples of both size-populations from Meyer Cave, 300 miles west



of Welsh Cave, and with the much larger individuals referred to *B. b. brevicauda* from Robinson Cave, Tennessee, 110 miles south of Welsh Cave.

Only one measurement could be taken on the smaller mandible fragment CM 20145: Depth of mandible at  $M_3$ —1.6 mm. The same measurement for the larger mandible CM 20144 was 2.3 mm.

TABLE 2. *Blarina brevicauda*, VARIOUS LOCALITIES, MEASUREMENTS IN MM.

Locality	$\bar{X}$	O. R.	N
Total length of mandible, including incisor			
Welsh Cave, Kentucky, CM 20144	15.3	—	1
Meyer Cave, Illinois*			
<i>B.b. cf. carolinensis</i>	12.6	12.0-13.4	134
<i>B.b. cf. brevicauda</i>	14.8	14.0-16.0	93
Robinson Cave, Tennessee**			
<i>B.b. cf. brevicauda</i>	17.2	15.6-18.3	21
Length, C— $M_3$			
Welsh Cave, Kentucky, CM 20144	6.1	—	1
Meyer Cave, Illinois*			
<i>B.b. cf. carolinensis</i>	5.5	5.2-5.7	134
<i>B.b. cf. brevicauda</i>	6.2	5.9-6.6	93
Width of mandibular condyle			
Welsh Cave, Kentucky, CM 20144	4.1	—	1
Meyer Cave, Illinois*			
<i>B.b. cf. carolinensis</i>	3.2	3.1-3.4	134
<i>B.b. cf. brevicauda</i>	3.9	3.7-4.1	91

\*Data from Parmalee, 1967.

\*\*Data from Guilday, Hamilton & McCrady, 1969.

### Vespertilionidae

#### *Myotis* Kaup, ?species—Little brown bat

MATERIAL: CM 20150: 1 right mandible with  $M_2$ – $M_3$ .

REMARKS: Beyond the statement that the specimen falls within the size range of the *M. lucifugus/sodalis/austroriparius/subulatus* size group, this specimen cannot be identified. Measurements are: Mandible length—9.5 mm; canine through  $M_3$ —5.4 mm.

#### *Pipistrellus cf. subflavus* (Cuvier)—Pipistrelle

MATERIAL: CM 20151. 1 left mandible with  $M_3$ ; 1 left mandible, no dentition.

REMARKS: Measurements follow: From anterior border of canine alveolus to posterior border of  $M_3$ —4.4 mm. and 4.6 mm.; alveolar measurement,  $P_4$ – $M_3$ —3.6 mm. and 3.6 mm.

## Leporidae

*Lepus americanus* Erxleben—Snowshoe hare

MATERIAL: CM 20202. 1 left humerus, 1 right innominate, 1 right femur minus proximal head, 1 metatarsal.

REMARKS: The only lagomorphs presently recorded from Kentucky are the ubiquitous common cottontail (*Sylvilagus floridanus*), the New England cottontail (*S. transitionalis*) in extreme eastern Kentucky, and the swamp rabbit (*S. aquaticus*) in western Kentucky. In the first two species the limb bones are smaller and shorter. In all three species they are relatively more robust than in *Lepus americanus*. Comparison was made with larger forms of *Lepus*, but they were too large to be considered.

This is the first record of the snowshoe hare from Kentucky. It does not occur any farther south than southern Michigan and extreme northeastern Pennsylvania in the plateau area, some 300 miles north of Welsh Cave, although it has been taken as far south as White Rock, Tennessee, in the southern Appalachians (Kellogg, 1939). Its presence in the Welsh Cave local fauna is not unexpected, but complements the occurrence of other boreal forms in the fauna.

## Sciuridae

*Spermophilus tridecemlineatus* (Mitchill)—Thirteen-lined ground squirrel

MATERIAL: CM 12627, 12890-12913, 12963, 20014-20015, 20155-20183. 39 left, 38 right mandibles; 7 left, 10 right maxillae; isolated molars and post-cranial material.

REMARKS: Remains of 90 individual small mammals were recovered. Forty-three, or approximately 50% of them, were thirteen-lined ground squirrel. This prairie ground squirrel does not occur in Kentucky at the present time. Welsh Cave lies about 200 miles south of its present range (from central Ohio, west to Wyoming, north to central Manitoba, south to Texas, but avoiding the Mississippi Valley). It does not occur in forests of the East and the South. Its presence, based upon its modern habits, is indicative of a former prairie or semi-prairie environment at the time of deposition. The large number of individuals indicates that conditions were congenial for it. During the early post-Pleistocene, this squirrel had an extensive distribution east of its present range. Pleistocene remains are known from New Paris No. 4 and Bootlegger Sink, Pennsylvania; Eagle Rock, West Virginia (CM collection); Natural Chimneys, Virginia; and Robinson Cave, Tennessee. Pre-Wisconsinan remains are known from Cumberland Cave, Maryland, and Trout Cave,

West Virginia (CM collection). It has also been reported from an Indian site in northeastern Arkansas dated at about 1200 A.D., some 200 miles east of its present range, in the Mississippi Lowlands (Guilday and Parmalee, in press). The extensive range withdrawal indicated within the past 13,000 years by the thirteen-lined ground squirrel is graphic testimony to the major range adjustments of the continental element of the eastern late Pleistocene fauna as the climate ameliorated and forest cover increased.

*Tamiasciurus hudsonicus* (Erxleben)—Red squirrel

MATERIAL: CM 20153. 1 incisor.

REMARKS: The red squirrel has not been recorded from Kentucky during Recent times, although it occurs just across its northern border in Indiana, and has been taken as far south in the Appalachian Mountains as eastern Tennessee (Hall and Kelson, 1959, 1:400). Although only one incisor was recovered from Welsh Cave, remains of at least four individuals were recovered from undated, but presumed late Pleistocene, cave sediments at Savage Cave, Kentucky, 150 miles southwest of Welsh Cave (CM 12983). This species has been recorded from at least four cave deposits and one archeological site in Tennessee (summarized in Guilday, Hamilton, and McCrady, 1969). It also reached the Ozark Mountains of Arkansas during Pleistocene times (Brown, 1908). The red squirrel is the most terrestrial "tree" squirrel and may often be found living in burrows even in unforested areas. It does not, however, wander far from tree cover, but appears to be more adaptable than the larger tree squirrels or the flying squirrels in that respect.

Geomyidae

*Geomys* cf. *bursarius* (Shaw)—Plains pocket gopher

MATERIAL: CM 12918, 12962, 20152. 3 left, 3 right mandibles; 2 incisors; 1 premolar; 1 partial skull; 3 femora; 2 humeri.

REMARKS: Specific identification was not possible. Welsh Cave lies approximately 300 miles southeast of the modern range of the plains gopher [*Geomys bursarius* (Shaw)] and perhaps 400 miles north of the range of the southeastern gopher, *Geomys pinetis* Rafinesque (see fig. 31). The lower Mississippi Valley lowlands appear to act as a barrier to both species. *Geomys bursarius* does not now occur east of the Ohio-Mississippi drainage. The two species approach to within approximately 250 miles of each other in the Louisiana-Mississippi-Alabama area, again separated by the Mississippi River Valley. Some evidence for the former



expansion of the range of *G. bursarius* is the presence of this species at Modoc Cave, southwestern Illinois, 35 miles south of its present range (Parmalee and Hoffmeister, 1957:261), at least 3000 years ago. Presence of pocket gopher remains east and south of the Ohio River, in central Kentucky, present an interesting problem. Do they imply a former range continuum between the now disjunct ranges of *G. bursarius* and *G. pinetis*, implying a post-glacial differentiation of these two species? The main osteological difference between the two forms is in the shape of the nasal bone. Hall and Kelson (1959, 1:448) characterize the nasals of *G. bursarius* as "not hour-glass shaped (only slightly, if at all, constricted near middle)." The eastern species, *G. Cumberlandensis*, *fontanelus*, *colonus*, and *pinetis* are characterized thus: "nasals hour-glass shaped, strongly constricted near middle." However, two of these forms, *G. colonus* and *G. pinetis*, are further subdivided by the same character (*G. pinetis* nasals much constricted and *G. colonus* nasals little constricted at middle). *G. colonus*, confined to the coastal area of southern Georgia, is obviously recently derived from *G. pinetis* stock. The shape of the nasals is variable. Some specimens of *G. bursarius* closely approach those of *G. pinetis* in this character, suggesting a late differentiation, probably during early post-Pleistocene times.

*Geomys bursarius* is a prairie form, sensitive to the presence or absence of forest cover. Parmalee *et al* (1969:21) in discussing the presence of *G. bursarius* at Crankshaft Pit, near St. Louis, Missouri, state: "Remains . . . were common in the cave fill . . . 34 individuals . . . but because of encroachment of forest in the immediate vicinity of Crankshaft Cave—much of which was open pastureland 20 years ago—pocket gopher no longer occurs in the local area."

The fauna recovered from Welsh Cave suggests an open-prairie parkland environment at the time of deposition around 13,000 years ago, now replaced by dense deciduous forest that does not support *Geomys*. The Ohio-Mississippi river system is apparently a boundary today and must have been an even more effective one during that period of heavy glacial run-off attendant upon the melting of the continental glaciers. Although closer to the range of *G. bursarius* than to that of *G. pinetis*, there is no major physiographic barrier to prevent range adjustment to the south as there is in the big river systems to the north and west. The Welsh Cave stock may have retreated south to survive today in the open piny woods and sandy soil of southern Alabama, Georgia, and Florida.

*Geomys bursarius* ranges north into Canada in prairie or semi-prairie



areas avoiding dense forests on one hand and the short-grass plains to the west on the other. One is tempted, then, to include *Geomys* as a portion of the boreal fauna contemporaneous with the larger extinct mammals, and if its affinities do prove to lie with *G. pinetis* (only better fossil material may resolve that), one is further tempted to state that the northern boundary of *G. pinetis* today is determined not by temperature but by the distribution of dense deciduous forest. Pocket gopher remains were also recovered from an undated but presumed late Pleistocene deposit at Savage Cage, Logan County, Kentucky, 150 miles southwest of Welsh Cave (3 individuals, CM collection). They were conspicuously absent, however, from the Robinson Cave local fauna, Overton Co., Tennessee, 110 miles south of Welsh Cave. Although boreal elements were common to both caves, Robinson Cave was distinctly higher in forest forms, and may have been locally unsuitable for gophers. As an example, the remains of 26 tree squirrels, but only 3 thirteen-lined ground squirrels, were recovered from Robinson Cave. At Welsh Cave, however, the ratio of thirteen-lined ground squirrels to tree squirrels was 43 to one.

In summary, until more suitable fossil material is recovered, specimens from Welsh Cave cannot be identified to species. Further discoveries, however, should aid in reconstructing the late Pleistocene history of the genus *Geomys*.

#### Cricetidae

##### *Clethrionomys gapperi* (Vigors)—Red-backed vole

MATERIAL: CM 20008. 1 M<sup>2</sup>.

REMARKS: This nominally northern vole, confined to transition and Canadian Zone forests in the Appalachian area, occurs as far south as northern Georgia in the higher mountains. It has been recorded from Black Mountain, Harlan County, Kentucky, 135 miles southeast and 3,200 feet higher in elevation than Welsh Cave, but does not occur in central or western Kentucky at the present time (Hall and Kelson, 1959). The red-backed vole represents another boreal element in the fauna. In the American Midlands the southern border of its range lies in central Wisconsin and northern Michigan. It has been found as a sub-fossil at Meyer Cave, southwestern Illinois, 300 miles west of Welsh Cave.

##### *Phenacomys* cf. *intermedius* Merriam—Spruce vole

MATERIAL: CM 20007. 1 left M<sup>1</sup>.

REMARKS: This is the first Kentucky record for the spruce vole. Now an inhabitant of the Canadian and Hudsonian Life Zones, *Phenacomys* is found no farther south, in eastern North America, than the northern shores of Lake Superior and the St. Lawrence River. It has been recorded from Pleistocene sites in the Appalachian Mountains from central Pennsylvania (New Paris No. 4 C-14,  $11,300 \pm 1000$  years B.P.), south to eastern Tennessee (Guy Wilson Cave C-14,  $19,700 \pm 600$  years B.P.). Although represented by a single upper first molar, the identification, based upon presence of roots, absence of cement and general size and configuration of the tooth, is unequivocal in this case. This implies a recession in range of at least 500 miles to the north since late Pleistocene times.

*Microtus cf. pennsylvanicus* (Ord)—Meadow vole

MATERIAL: CM 12917, 20010, 20012, 20188-20192. 6 left, 11 right mandibles; 1 left, 2 right maxillae; 1 skull.

REMARKS: With the exception of 13 identified individuals of what is probably the pine vole, this is the commonest microtine at the site and far outnumbers such woodland types as *Clethrionomys* and *Phenacomys*. This species is found from coast to coast, north to the tundra. The site lies just north of its present southern limits. Its presence in such high relative numbers reinforces the general picture of grasslands of some type at the time of deposition. *Microtus pennsylvanicus*, however, is an extremely adaptable animal. Colonies may be found in small grassy enclaves scattered throughout forest situations, as well as in moist prairie habitats. Only three mandibles were sufficiently well preserved to measure the dentition:  $M_1$ - $M_3 = 6.2$  mm, 6.2 mm, 6.2 mm.

*Microtus xanthognathus* (Leach)—Yellow-cheeked vole

MATERIAL: CM 12914-12915, 20011, 20186-20187. 1 left, 1 right mandible; 2 partial skulls; 1  $M^3$ ; 1 tibia.

REMARKS: Although the present range of this large vole lies in the Hudsonian Zone of western Canada north of latitude 50 (fig. 31), it was apparently common in the late Pleistocene of the Appalachian Mountains. It has been recorded from Bootlegger Sink and New Paris No. 4 in Pennsylvania, Eagle Rock Cave, West Virginia, and Natural Chimneys, Virginia. This is the first Kentucky record and the first one from the Cumberland Plateau. Neither *Microtus xanthognathus* nor *Phenacomys* occurred in the extensive small mammal fauna of Robinson Cave, Tennessee, 110 miles to the south. Remains of this species have also been



Fig. 9. *Canis dirus* Leidy, ventral view of cranium, CM 12625, Welsh Cave, Woodford County, Kentucky. Scale in centimeters.





Fig. 10. *Canis dirus* Leidy, lateral view of cranium, CM 12625, Welsh Cave, Woodford County, Kentucky. Scale in centimeters.



recovered from Meyer Cave, Illinois, and Bat Cave, Missouri (collections of Central Missouri State College).

*Pitmys* McMurtrie (or *Pedomys* Baird)—Pine or prairie vole

MATERIAL: CM 20009, 20013, 20193-20197. 13 left, 9 right mandibles and  $M_1$ 's.

REMARKS: Both the pine vole and the prairie vole inhabit central Kentucky. The prairie vole is a grasslands form and the pine vole a burrowing form, whose distribution is governed more by soil conditions than by type of ground cover. The conditions of excavation do not guarantee the contemporaneity of all the remains, especially those of small mammals, at the site. Neither of these forms, based solely upon their present distribution, i.e., absent from all but the southern parts of Minnesota and Wisconsin, would be expected to be components of a boreal fauna, although both do reach, at least locally, into the Canadian Life Zone.

Erethizontidae

*Erethizon dorsatum* (Linnaeus)—Porcupine

MATERIAL: CM 12654, 20199-20201. 2 partial skeletons with skulls.

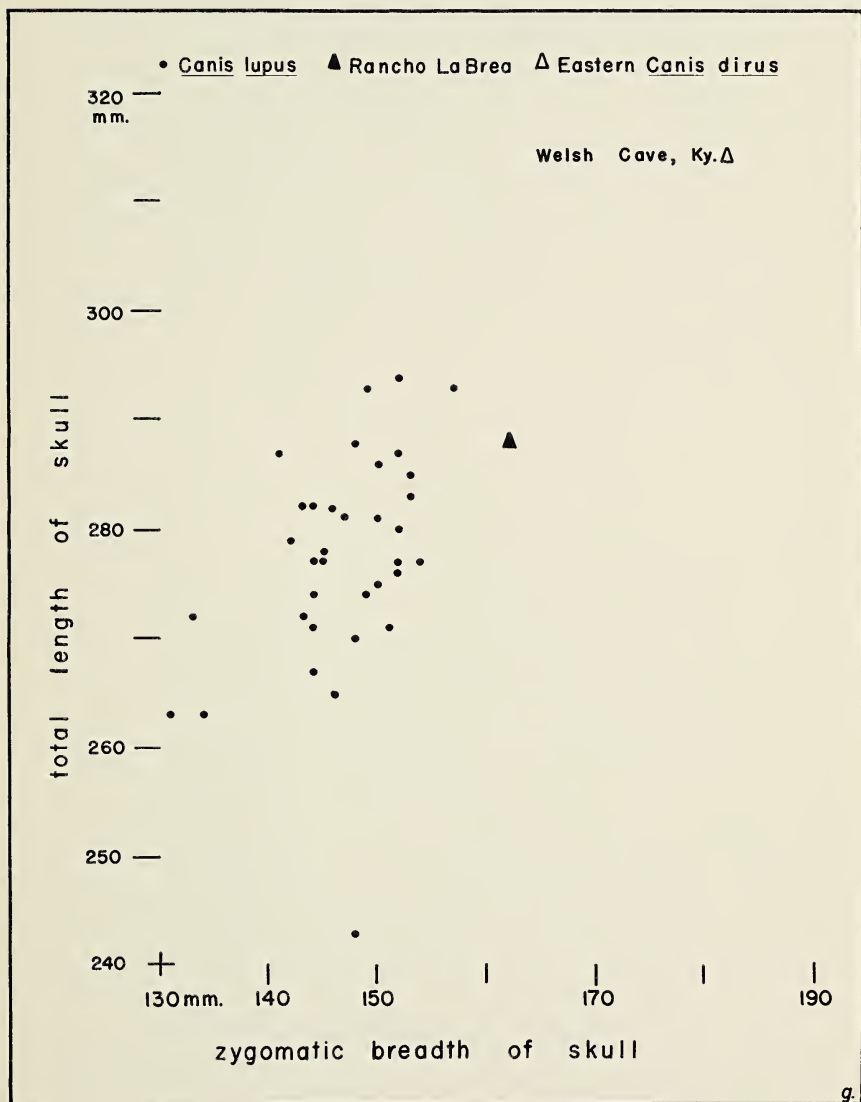
REMARKS: Contrary to the range map in Hall and Kelson (1959, 2:782), the porcupine is not a member of the modern Kentucky mammal fauna. It has been recovered from deposits at Savage Cave, Logan County, Kentucky, and from Pleistocene fossil sites as well as archeological sites in Tennessee (Parmalee and Guilday, 1966).

Canidae

*Canis dirus* Leidy—Dire wolf

MATERIAL: CM 12625 (figs. 9 and 10). 1 skull with zygomatic arch, incisors, canines, right  $P^1$ , left  $P^1$ ,  $P^2$  and half of  $P^3$  missing. Pterygoids missing; skull otherwise complete and uncrushed. Dentition moderately heavily worn. Right lower jaw with  $P_4$  and  $M_1$ , alveoli for  $P_1$ ,  $P_2$ ,  $P_3$ ,  $M_1$ , and  $M_2$ ; dentition lightly worn. One 4th cervical vertebra, 1 lumbar vertebra, 1 right humerus, 4 phalanges, 1 manubrium, 1 metatarsal fragment, 1 fragment of ilium.

REMARKS: At least two individual wolves are represented. The degree of tooth-wear on the lower jaw is not as far advanced as on the skull. The skull is in an excellent state of preservation. All cranial sutures are closed, and sagittal and lambdoidal crests are greatly developed. Tooth-wear indicates an aging adult: carnassial blades are blunted and flattened, but there is only moderate wear on  $M^1$  and none on  $M^2$ . Characteristic of *Canis dirus*, the upper  $P^4$  and  $M^1$  are large, exceedingly robust, and heavy-looking. The antero-internal cusp of  $P^4$  is very weakly developed, more characteristic of the norm for *C. dirus* than that of *C. lupus*. The



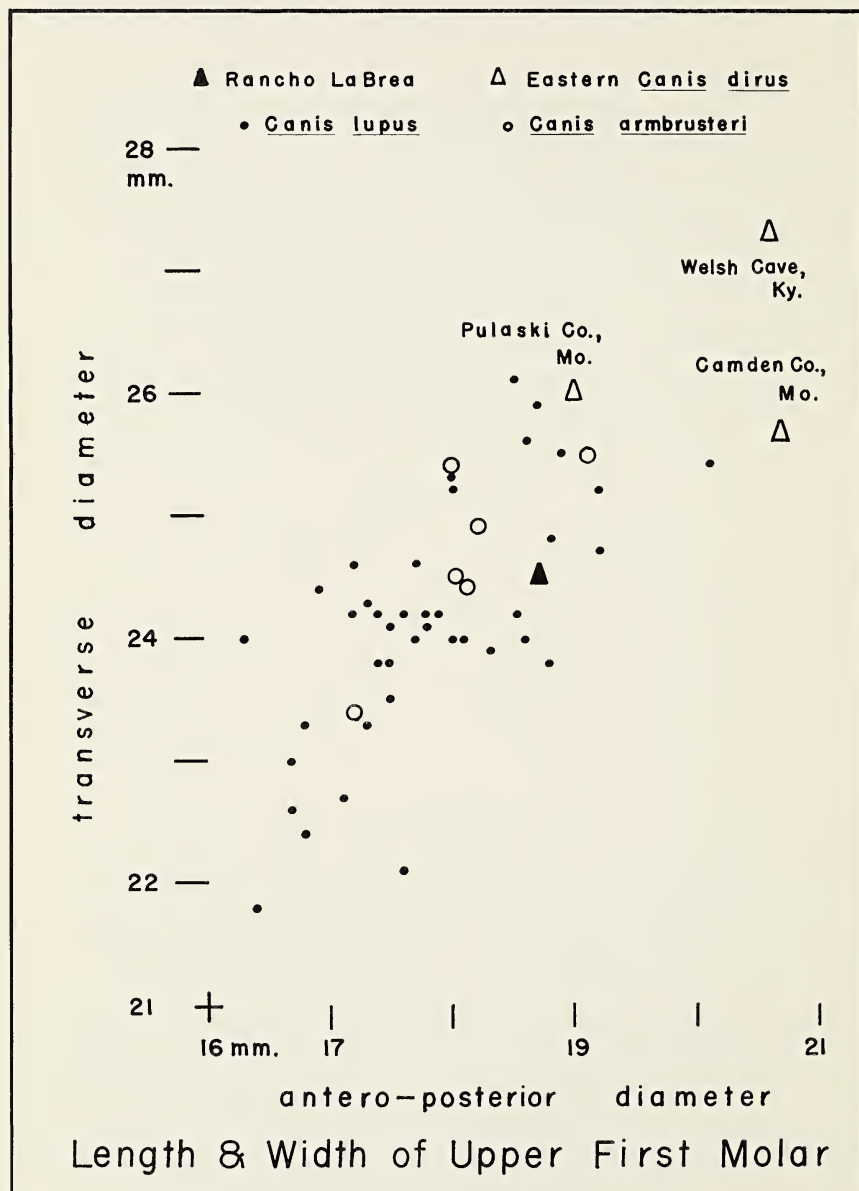


Fig. 12. Length x width of upper first molar. *Canis arnbrusteri* (pre-Wisconsinan); from Gidley & Gazin, 1938. *C. dirus* (Wisconsinan): Rancho La Brea, California, CM 3995; Welsh Cave, Kentucky, CM 12625; Pulaski County and Camden County, Missouri, Hawksley *et al.*, 1963. *C. lupus* (modern); from Young & Goldman, 1944.

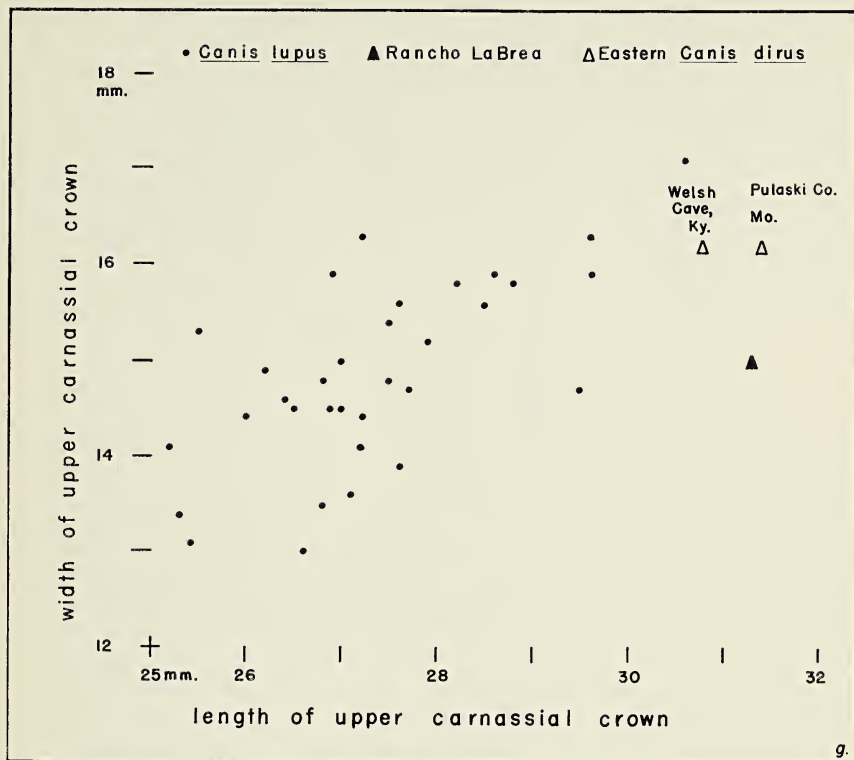


Fig. 13. Length x width of upper fourth premolar, *Canis lupus* (modern) and *C. dirus* (Wisconsinan). See caption, fig. 12, for source data.

antero-internal cingulum of  $M^1$  is greatly reduced. The position of the posterior palatine foramina; the relative shortness of the post-glenoid portion of the skull; the configuration of the squamosal border; and the projection of the inion agree with those characters pointed out by Young and Goldman (1944:399-400) as differentiating *C. dirus* from *C. lupus* or *C. niger*. Compared with *C. lupus*, the Welsh Cave skull is wide with a broad palate and a relatively narrow rostrum. Zygomatic breadth averaged 53% of total skull length in a sample of 15 skulls of *C. lupus* from Alaska (Young and Goldman, 1944:490). It measured 58% in the Welsh Cave skull and 56% in one skull of *C. dirus* from Rancho La Brea (CM 3995). An indication of the relative size of this skull can be seen in figs. 11, 12, and 13.



The major cranial characters differentiating *C. dirus* from *C. lupus* appear to be associated with excessive jaw development and hypertrophy of the dentition and the areas for the accommodation of the jaw musculature. The observation by Merriam (1912) that the post-glenoid portion of the skull is relatively short can perhaps be more readily visualized as another indication of the relative hypertrophy of the jaw region, i.e., the pre-glenoid portion of the skull is relatively longer in *C. dirus* [77.7% in *C. lupus* (DC 1247); 78.4% and 78.6% in *C. dirus* (CM 12625 and CM 3995 from Welsh Cave and Rancho La Brea)].

### Ursidae

#### *Ursus arctos horribilis* Ord—Grizzly bear

**MATERIAL:** CM 12617. Left maxilla with P<sup>4</sup>-M<sup>2</sup>; right frontal; left occipital; 1 adult canine; 1 immature canine.

**REMARKS:** Remains of two animals were recovered: one adult represented by a single canine, and a cub represented by the remaining material. The specimens and their significance were reported in Guilday, 1968. Grizzly bear remains have since been recovered from Organ Cave, Greenbrier County, West Virginia (CM 12999, 3 molars).

### Mustelidae

#### *Taxidea taxus* (Schreber)—Badger

**MATERIAL:** CM 12640. 1 temporal bone.

**REMARKS:** This is the first record for the badger from Kentucky. Its modern distribution parallels that of the thirteen-lined ground squirrel in the East. Badger remains have also been reported from Illinoian cave deposits in Pennsylvania (Port Kennedy Cave, Cope, 1899) and Maryland (Cumberland Cave, Gidley and Gazin, 1938).

### Elephantidae

#### *Mammuthus* Burnett, ?species—Mammoth

**MATERIAL:** CM 12628. 3 partial ribs; 2 fragments of thoracic vertebrae; 6 bone fragments; 1 molar fragment.

**REMARKS:** The tooth fragment is too small to be identified to species. The other 11 referred specimens are obviously proboscidean but beyond that nothing can be said.

TABLE 3. *Canis dirus*, SKELETAL MEASUREMENTS (IN MM.)

CM 12625, Welsh Cave, Kentucky (Carbon-14 date, 12,950  $\pm$  550 yrs. B.P.).  
 CM 3995, Rancho La Brea, Hancock County, California (CM 3996 mandible and CM 3997 mandible).  
 CMSC 100, Cave Pul-103, Pulaski County, Missouri, data from Hawksley, Reynolds & McGowan, 1963.  
 UM 2870, Cave Cam-001, Camden County, Missouri, data *ibid.*  
 SIU P-429, Powder Mill Creek Cave, Shannon County, Missouri (Carbon-14 date, 13,170  $\pm$  600 yrs. B.P.), data from Galbreath, 1964.

	CM 12625 (Welsh)	CM 3995 (La Brea)	CMSC 100 (Missouri)	UM 2870 (Missouri)	SIU P-429 (Missouri)
Cranial Measurements					
(Definitions from Young & Goldman, 1944, unless otherwise stated.)					
Paired elements measured separately where possible.)					
Greatest length of skull	314.0	288.0	—	—	—
Condyllo-basal length	288.0	262.0	—	—	—
Zygomatic breadth	182.0	162.0	—	—	—
Squamosal constriction	100.3	92.4	—	—	—
Width of rostrum	53.7	—	—	—	—
Interorbital breadth	66.6	57.9	—	—	—
Least postorbital width, cranium	56.4	47.6	—	—	—
Width across postorbital processes	104.0	82.4	—	—	—
Width of foramen magnum	26.9	23.2	—	—	—
Glenoid fossa to condyle	62.3	56.0	—	—	—
Distance from a line between postorbital processes toinion (from Gidley & Gazin, 1938)	54.0-52.3	43.8-42.0	—	—	—
Internal diameter, external nares	30.5	32.4	—	—	—
Maximum width internal nares at palate	27.1	—	—	—	—
Maximum width across canine alveoli	58.6	56.2	—	—	—
Width of rostrum across infra-orbital foramina	63.9	66.3	—	—	—
Long diameter auditory bulla (Hawksley <i>et al.</i> , 1963)	32.9-34.6	31.9-32.2	32.2	30.0	—
Maximum width of skull between anterior roots of P <sup>4</sup> 's	93.8	84.7	—	—	—

TABLE 3. *Canis dirus*, SKELETAL MEASUREMENTS (continued)

	CM 12625 (Welsh)	CM 3995 (La Brea)	CMSC 100 (Missouri)	UM 2870 (Missouri)	SIU P-429 (Missouri)
Cranial Measurements (continued)					
Maximum width of skull between posterior roots of P <sup>4</sup> 's	99.6	91.9	—	—	—
Length of palate, midline, anterior end of pre- maxilla to palatine spine	154.3	145.0	—	—	—
Length, incisive foramina	19.0-19.0	16.0-16.0	—	—	—
Maximum width, upper incisor tooththrow I <sup>3</sup> -I <sup>3</sup>	40.4	37.8	—	—	—
Maxillary tooththrow, anterior border of canine alveolus to posterior border of M <sup>2</sup>	133.0-132.0	121.0-123.0	—	—	—
Length of tooththrow, P <sup>1</sup> -M <sup>2</sup>	108.0-107.0	98.0-98.0	—	—	—
Upper canine alveolus, antero-posterior	19.2	18.0-17.4	—	17.7	—
Upper canine alveolus, transverse diameter	13.0	12.6-11.5	—	12.7	—
P <sup>1</sup> , antero-posterior diameter	—	9.8	—	—	—
P <sup>1</sup> , transverse diameter	—	6.6	—	—	—
P <sup>2</sup> , antero-posterior diameter	14.9	—	—	—	—
P <sup>2</sup> , transverse diameter	7.7	—	—	—	—
P <sup>3</sup> , antero-posterior diameter	18.3	18.0	19.8	19.0-17.8	—
P <sup>3</sup> , transverse diameter	8.3	7.6	8.9	9.0-8.2	—
P <sup>4</sup> , antero-posterior diameter, outer side	30.8-30.8	31.2-31.3	33.2	32.0-32.0	—
P <sup>4</sup> , maximum transverse diameter	16.2-15.4	15.0-14.1	16.4	—	—
P <sup>4</sup> , transverse diameter behind antero-cone	14.2-14.1	12.7-12.4	14.0	14.0-13.0	—
M <sup>1</sup> , antero-posterior diameter	20.6-20.6	18.6-18.7	20.7	19.0	—
M <sup>1</sup> , transverse diameter	27.3-27.0	24.5-24.3	25.7	26.9	—
M <sup>2</sup> , antero-posterior diameter	10.9-10.0	8.7-8.0	12.0	11.0	—
M <sup>2</sup> , transverse diameter	15.5-15.2	14.0-13.9	16.2	16.0	—

TABLE 3. *Canis dirus*, SKELETAL MEASUREMENTS (continued)

	CM 12625 (Welsh)	CM 3995 (La Brea)	CMSC 100 (Missouri)	UM 2870 (Missouri)	SIU P-429 (Missouri)
Mandibular Measurements (Definitions from Gidley & Gazin, 1938)					
Depth of jaw below heel of M <sub>1</sub>	33.4**	33.9-35.0*	40.0	—	35.5
Thickness of jaw below heel of M <sub>1</sub>	16.1	15.9-16.6	—	—	18.3
P <sub>4</sub> , antero-posterior diameter	19.6	18.2-19.1	20.2	—	19.5
P <sub>4</sub> , transverse diameter	9.9	9.3-10.3	10.5	—	9.5
M <sub>1</sub> , antero-posterior diameter	36.8	31.8-34.9	36.9	—	34.7-34.9
M <sub>1</sub> , transverse width trigonid	13.5	12.4-13.3	—	—	13.6-13.7
M <sub>1</sub> , transverse width talonid	13.4	10.9-13.0	—	—	—
M <sub>2</sub> , antero-posterior diameter	—	—	14.0	—	13.9-14.0
M <sub>2</sub> , transverse diameter	—	—	11.4	—	10.0-10.0
Humerus Measurements (Definitions from Galbreath, 1964)					
Length	236.8 est.	—	—	252.0	247.0 est.
Head, antero-posterior diameter	64.7	—	—	67.3	68.±
Mid-point of shaft, antero-posterior diameter	24.2	—	—	—	24.5
Mid-point of shaft, transverse diameter	—	—	—	—	23.8
Distal end, transverse diameter	53.2	—	—	56.0	56.2-57.5

\* = CM mandibles 3996 and 3997, different individuals.

\*\* = Skull and mandible from different individuals.

## Tayassuidae

*Platygonus compressus* LeConte—Flat-headed peccary

MATERIAL: At least 1183 specimens representing a minimum of 31 individuals and including the following: whole or partial skulls, 21; mandibles, including left and right elements, 59 (minimum number of individual peccaries estimated from complete mandibles or fragments); cervical vertebra, 44; thoracic vertebra, 93; lumbar vertebra, 54; sacrum, 16; caudal vertebra, 13; sternebra, 29; scapula, 36; humerus, 50; radius/ulna, 45; scaphoid, 13; semilunar, 17; cuneiform, 6; pisiform, 6; os magnum, 8; unciform, 11; metacarpal III, 30; metacarpal IV, 32; fused metacarpal III and IV, 2; os innominatum, 29; femur, 41; patella, 20; tibia, 28;



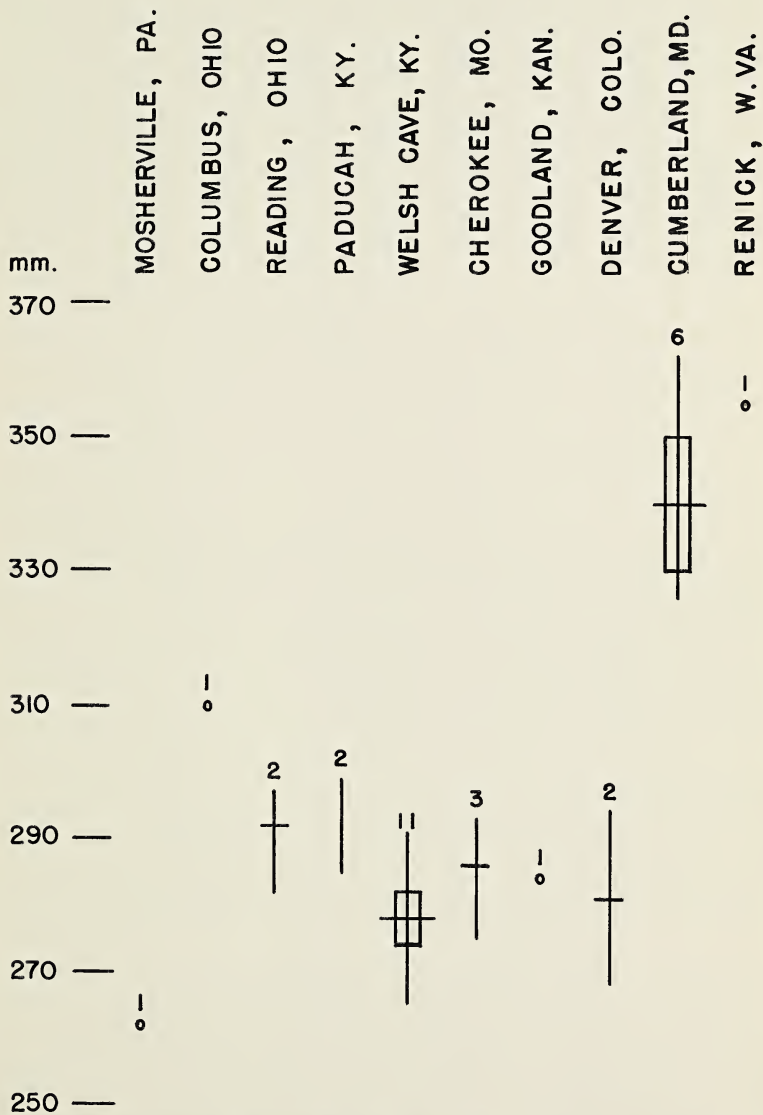
fibula, 47; cuboid, 16; navicular, 14; internal cuneiform, 2; astragalus, 25; calcaneum, 23; fused metatarsal III and IV, 27; vestigial lateral metapodial, 9; proximal phalanx, 79; 2nd phalanx, 74; distal phalanx, 50; plus rib fragments, hyoid elements and sesamoids; catalogued under the following numbers: CM 12624; 12630-12639; 12641-12653; 12656-12657; 12684; 12885-12889; 12921-12960; 20113-20141. One composite skeleton was donated to the Illinois State Museum, Springfield, Illinois. The remaining material is in the Carnegie Museum collection.

**GENERAL REMARKS:** *Platygonus compressus* survived to a radiocarbon age of at least  $11,900 \pm 750$  years B.P. (Ray, *et al.*, 1970). [The C-14 date of the Sandusky, Ohio, find,  $4,290 \pm 150$  years B.P. (M-1516; Hoare, 1964) is unacceptable from its geological context]. Remains of this species are probably the commonest of all large Pleistocene mammals recovered from eastern and central North American cave deposits. These peccaries are known to have ranged from Mexico north into periglacial environments and apparently had a wide environmental tolerance. Despite their frequency in late Pleistocene deposits, peccary remains have not been identified from bone refuse from any North American archeological sites. The genus also occurred in temperate South America and may have survived there until a later time period. Bones of *Platygonus carlesi-wagneri* Rusconi have been reported from pre-Hispanic archeological deposits in association with funeral urns, artifacts, and a large modern mammal fauna from Santiago del Estero, Argentina (Rusconi, 1931:228-241).

The Welsh Cave peccary collection indicates a relatively homogenous population which appears to fall well within the range of variation of *Platygonus compressus* LeConte (see measurements and figs. 14, 15, 16, and 17). It agrees closely with that from Cherokee Cave, Missouri (Simpson, 1949), and with smaller collections from eastern North America, but is significantly smaller than the *Platygonus* sample from Laubach Cave, Texas (Slaughter, 1966), specimens of *P. cumberlandensis* from Cumberland Cave, Maryland, and Renick, West Virginia; and *P. vetus* from Mifflin, Pennsylvania (Leidy, 1882). Little is known

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Fig. 14. Condylobasal length of skull, various North American samples of *Platygonus*. *P. compressus* (early post-Wisconsinan): Mosherville, Pennsylvania (Ray *et al.*, 1970); Columbus, Ohio; Reading, Ohio (Frank Whitmore measurements); Paducah, Kentucky (Frank Whitmore measurements); Welsh Cave, Kentucky; Cherokee Cave, Missouri; Goodland, Kansas; Denver, Colorado. *P. cumberlandensis* (pre-Wisconsinan, probably Illinoian); Cumberland Cave, Maryland, and Renick, West Virginia. All measurements by Dr. Elaine Anderson unless otherwise specified. Symbol explanations fig. 17.



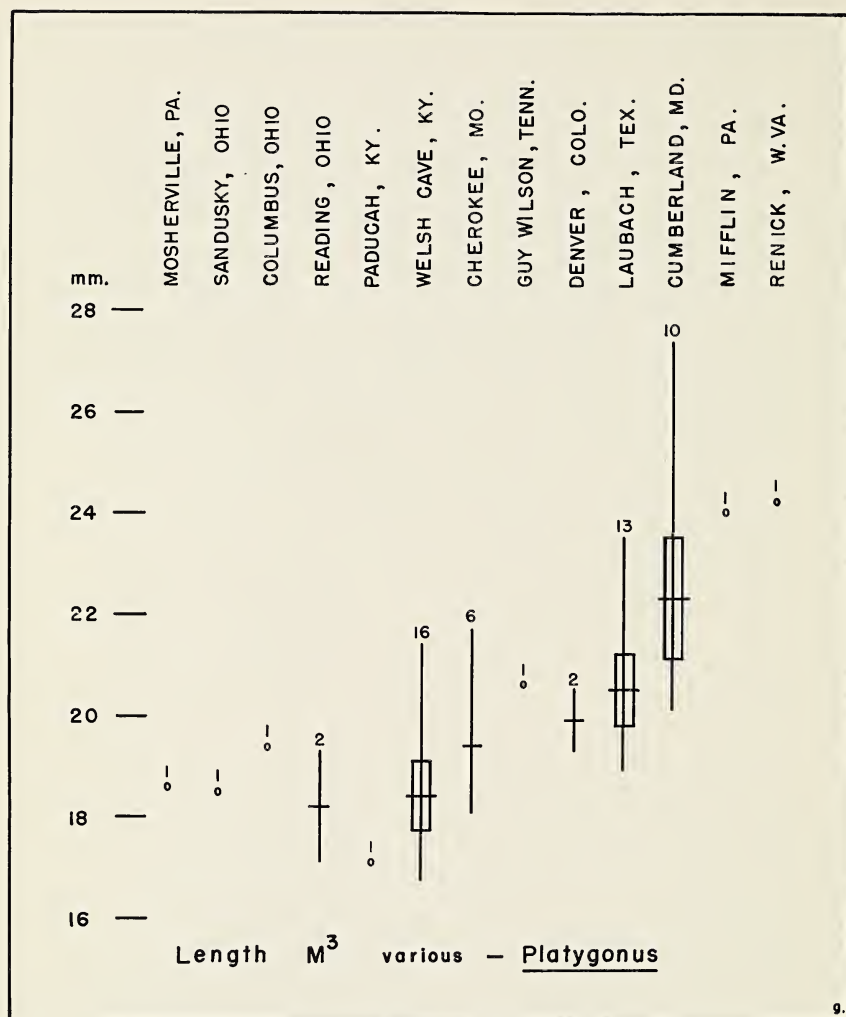


Fig. 15. Length of upper third molar, various North American samples of *Platygonus*. *P. compressus* (early post-Wisconsinan): Mosherville, Pennsylvania (Ray, *et al.*, 1970); Sandusky, Ohio (Hoare, 1964); Columbus, Ohio; Reading, Ohio (Frank Whitmore measurements); Paducah, Kentucky (Frank Whitmore measurements); Welsh Cave, Kentucky; Cherokee Cave, Missouri; Guy Wilson Cave, Tennessee; Denver, Colorado. *P. cumberlandensis* (pre-Wisconsinan, probably Illinoian): Cumberland Cave, Maryland, and Renick, West Virginia. *P. vetus* (Illinoian?): Mifflin, Pennsylvania (Leidy, 1882). All measurements by Dr. Elaine Anderson unless otherwise specified. Symbol explanation, fig. 17.

about temporal or geographic variation within this genus, but finds of *Platygonus* are so common and widespread throughout temperate North America that such information will become accessible as collections increase and dating techniques become more precise.

The flat-headed peccary was the commonest large mammal in the Welsh Cave local fauna, represented by a minimum of 31 animals ranging from a piglet to dentally senile adults.

**INDIVIDUAL AGE:** Skulls and mandibles of *Platygonus compressus* from Welsh Cave, Kentucky, and Cherokee Cave, Missouri, and of *Platygonus cumberlandensis* from Cumberland Cave, Maryland, were aged individually by degree of tooth replacement and wear. They were separated into eight age classes defined as follows:

1. Deciduous molars erupting.
2. Deciduous molars erupted— $M_1^1$  erupting.
3.  $M_1^1$  erupted, not worn;  $M_2^2$  erupting.
4.  $M_{1-2}^{1-2}$  erupted;  $M_3^3$  erupting;  $M_1^1$  beginning to wear.
5.  $M_3^3$  erupted;  $M_1^1$  moderate wear.
6. Permanent dentition fully in place;  $M_1^1$  extensive wear.
7. All teeth worn;  $M_1^1$  cusps worn smooth.
8. Cusps of cheek teeth worn smooth.

Actual ages of course are unknown, but judging by the toothwear and eruption schedules of its living relative, the collared peccary (Kirkpatrick and Sows, 1962:216), age class 2, is estimated at approximately 21 weeks; age class 3, about 43 weeks; age class 4, about 83 weeks. The collared peccary may live as long as 12 years, but the majority probably die before they are 7 or 8 (Lyle K. Sows, letter).

TABLE 4. RELATIVE AGE CLASSES, *Platygonus compressus* AND *Platygonus cumberlandensis*

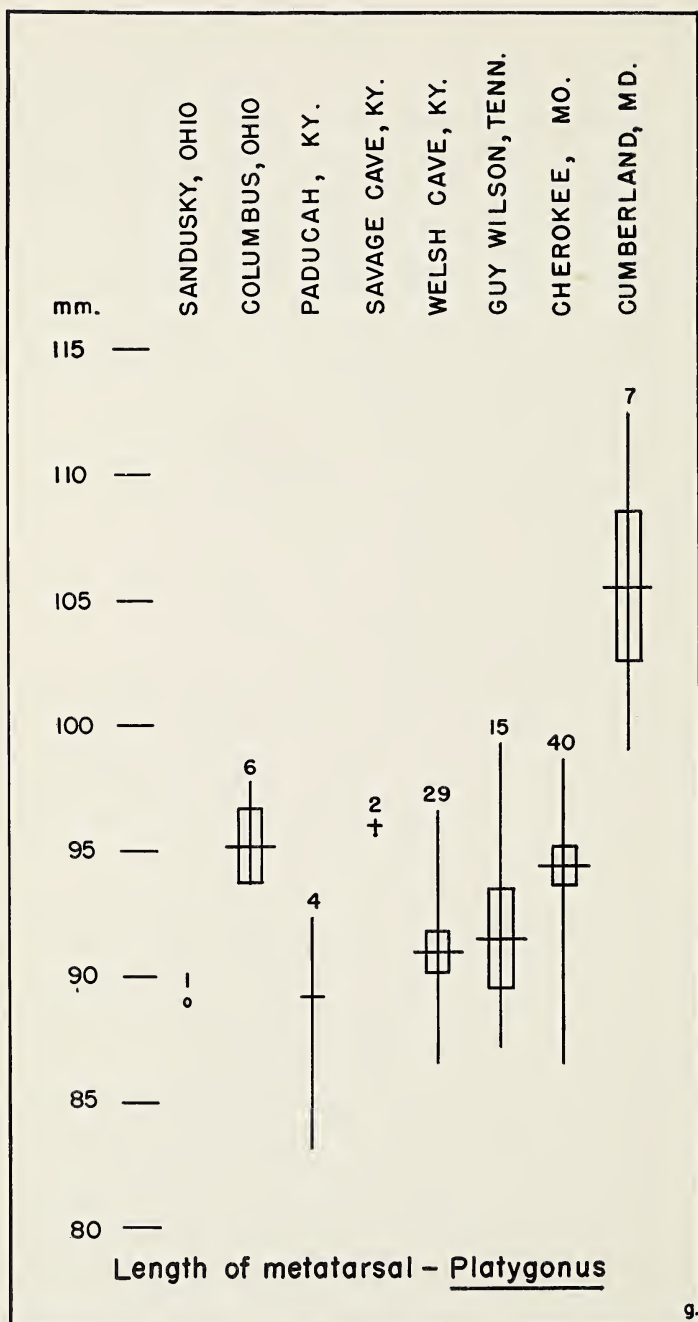
Locality	Age Classes																	
	Skulls									Mandibles								
	1	2	3	4	5	6	7	8	N	1	2	3	4	5	6	7	8	N
Welsh Cave,*	—	—	2	7	6	9	3	—	27	1	—	5	5	2	9	9	—	31
Kentucky																		
Cherokee Cave,*	—	—	2	4	—	2	4	1	13	—	—	4	5	—	1	7	1	18
Missouri																		
Cumberland Cave,**	—	—	1	3	3	5	3	—	15	—	—	5	2	1	4	1	—	13
Maryland																		
Totals	—	—	5	14	9	16	10	1	55	1	—	14	12	3	14	17	1	62

\**Platygonus compressus*.

\*\**Platygonus cumberlandensis*.

Age classes based on tooth-wear (defined above).





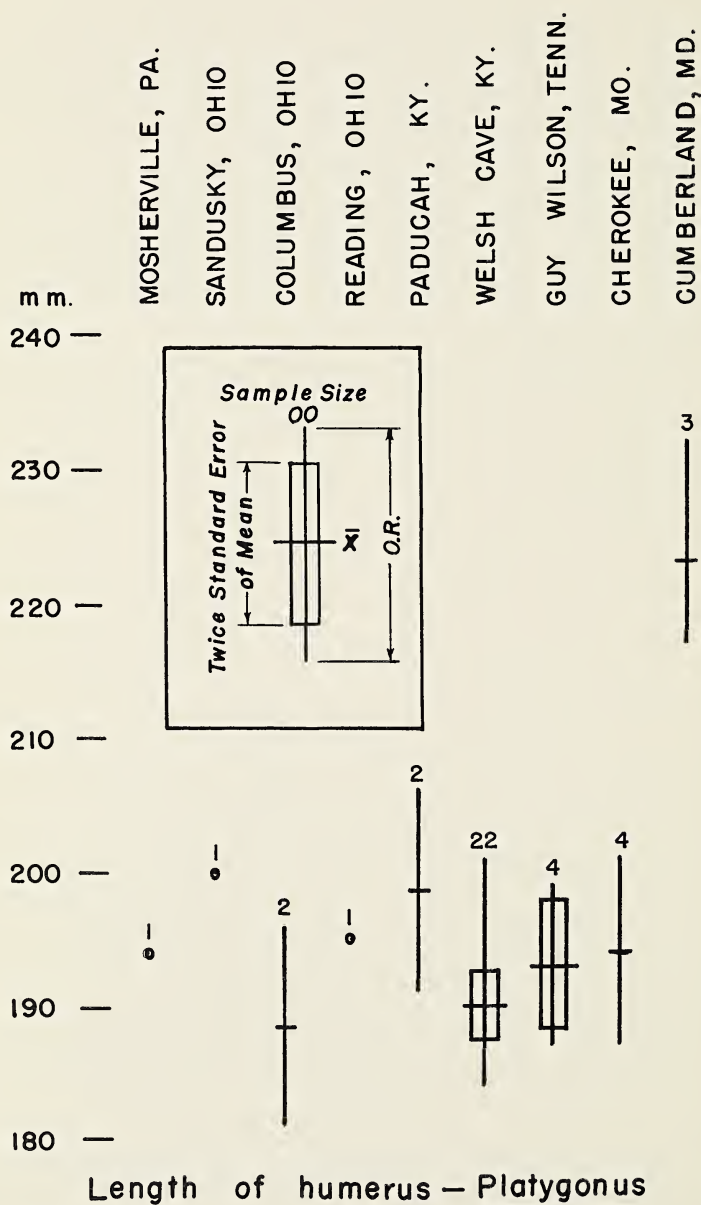
Note from table 4 that most of the peccaries from the three collections are adult animals. The living collared peccary reaches adult size at about 40 weeks of age, essentially our class 3, at which time both sexes are sexually mature (females at about 33 weeks of age, males at about 46 weeks). Deciduous premolars are not shed until about the 74th week, although this is variable. Kirkpatrick and Sows noted that deciduous premolars were shed from week 66 to week 83.

Aging by relative toothwear classes is a subjective procedure. All aging was done by one person (Anderson) in an attempt to reduce the extent of personal bias. Hence, no matter what the age relationship between modern and fossil peccaries, the three fossil groups should be comparable to each other.

The collared peccary is mainly a tropical animal and breeds throughout the year, although reproduction appears to be influenced, at least in the desert country of Arizona, by periods of drought and availability of food. It is unlikely that the extinct *Platygonus* bred throughout the year in temperate North America. They are known to have ranged almost to the Wisconsinan ice margin (Ray, *et al.*, 1970). The one immature mandible from Welsh Cave (CM 12960) is about three weeks of age, an estimate based upon tooth eruption in the collared peccary. The milk canine is fully erupted (it erupts at birth in *Tayassu*) and  $dM_{2-3}$  are erupting. (In the collared peccary, piglets are weaned at between six and eight weeks of age.) It is possible that immature animals are under-represented in samples like these, because of the fragility of the bones and their chance of being overlooked or ignored by the excavator. Although we know that adults of all ages are represented, we can say little about the composition of the population from which these samples were drawn. Sample size is small, and there is no real assurance that the time interval between age classes is the same. This may account for the dip in numbers of class-5 specimens found in Welsh Cave, or it may simply represent a shorter time expanse than classes on either side, and this may be the reason for the observed bimodality.

Not only is the duration of the breeding season unknown, but also the time, or times, of the year when the individual members of these cave

←  
Fig. 16. Length of metatarsal, various North American samples of *Platygonus compressus* (Sandusky, Columbus, Paducah, Savage Cave°, Welsh Cave, Guy Wilson Cave, Cherokee Cave) and *P. cumberlandensis* (Cumberland). See caption, fig. 15, for locality details, fig. 17 for symbol explanation. °Logan Co., Ky. CM collection.



samples met their deaths. There is no way of knowing whether this is a true population sample at any one time or whether age-class numbers are influenced by varying times of death and birth. It is perhaps noteworthy that numbers of all presumed-adult age classes are well represented except those of class 8, representing obviously senile animals.

**SEXUAL AND AGE VARIATION:** The most variable cranial dimensions were development of canine buttresses and suborbital zygomatic flare. Both areas are associated with fighting. The major defensive and, in fights with other peccaries, offensive weapon of modern tayassuids is the lower canine. This was almost certainly so with *Platygonus* as well. The primary offensive thrust is delivered out and up. This has produced specializations of cranial architecture designed to protect the animal, modifications which, in varying degrees, are found in suids (Ewer, 1958) as well as tayassuids. These can be seen in figures 29 and 30. The zygomatic flare beneath the orbit protects the eye; the postorbital zygomatic flare, the temporal musculature; the gonial flare, the masseter. The canine buttress not only serves to seat and protect the lower canine from damage when the mouth is shut, but also protects the ligaments of the snout musculature. (In the collared peccary, at least, some but not all these ligaments lie in the trough formed by the canine buttress on the side of the snout. See Woodburne, 1968:6, fig. 1.) The symphyseal keel on the ventral surface of the mandible (fig. 26-2B), present in *Platygonus* but not in modern tayassuids, served to strengthen the symphysis, which is relatively much narrower and not as long as in the collared peccary, because of the lengthening of the diastema in *Platygonus*.

It is not apparent whether the modifications discussed above vary with sex or age, although there is considerable variation in the Welsh Cave crania (fig. 29 and table 7). Modern collared peccaries do not form board-defended harems, and both living species exhibit no pronounced sexual cranial differences other than a general robustness of the male. The percentage of males to females in the Welsh Cave collection is not known. Despite the pronounced variations, the crania, with one exception, formed such a graded series that no decision was possible. The degree of variation could not be correlated with relative age as shown by increasing toothwear (table 7).



Fig. 17. Length of humerus, various North American samples of *Platygonus compressus* (Mosherville, Sandusky, Columbus, Reading, Paducah, Welsh Cave, Guy Wilson Cave, Cherokee Cave) and *P. cumberlandensis* (Cumberland). See caption, fig. 15, for locality details.



The exception was an unusually rugged partial skull preserving only the snout and the palate with dentition (CM 20113). This was one of the oldest specimens examined, with a dental age of 7 (see definition under "Individual Age" above), but other skulls almost as old (CM 12657, 12886, 12887) did not begin to approach it in rugosity. Although its dental measurements were not unusual, its rugosity and degree of canine buttress development were. To illustrate: the height of canine buttress in 12 individuals from Welsh Cave varied from 30.2 mm. to 37.5 mm., with a coefficient of variation of 6.62. CM 20113 measured 46.9 mm., 9.4 mm. larger than the range previously observed. The inclusion of this specimen in the sample boosted the coefficient of variation to 12.26 mm. (compare also width across canines with and without CM 20113). If this skull is indeed that of a male and its pronounced characters are attributed to sexual variation, then all other adult crania from the deposit might be construed as female. Perhaps a larger series would show some sexual bimodality, but with the exception of CM 20113, all other variation observed is probably an unresolvable mixture of both sexual and individual variation.

**ANATOMICAL MODIFICATIONS:** What can we surmise of the habitat requirements of *Platygonus*? We can perhaps extrapolate from the known ecology of the living peccaries by noting significant differences in body proportions and cranial and dental morphology. If these differences can be interpreted in terms of standard "morphological rules" that reflect the shaping force of the environment, then it may be possible to visualize, at least in part, the ecological demands of these extinct peccaries. Some excellent studies of cranial modifications of living mammals point to the feasibility of such an approach, e.g., Zeuner's (1935) on Rhinocerotidae, and Ewer's (1958) on living suids.

As will be discussed below, the anatomy of the flat-headed peccary suggests an open forest habitus. If this is so, it complements the marked prairie bias suggested by much of the accompanying fauna. This is not to suggest that the flat-headed peccary was a plains animal *sensu stricto*. It is suggested rather that it was not primarily a forest form.

The limbs (particularly their distal elements) are longer in *Platygonus* than in modern peccaries. Stride is increased by elongation of distal limb elements, and the speed of a complete limb cycle is increased by the relatively short humerus, bringing the area of insertion of the major propulsive muscles closer to the point of rotation at the shoulder. Relative limb proportions can be derived from table 5. In contrast with

*Tayassu*, the spinous processes of the thoracic vertebrae are relatively broader and more erect. The scapula of *Platygonus* is relatively larger, 99% of the length of the humerus in *Platygonus*, as compared to 95% in *T. tajacu* (G-823) and 90% in *T. pecari* (AMNH 80010). This combination of actual and relatively greater size of limb elements suggests that *Platygonus* was fleeter of foot than either of the modern forms. It appears to have been less cursorial than its contemporary, *Mylohyus*, but was further advanced along these lines than either of the two modern peccaries.

It has been suggested that *Mylohyus* in the New World is the ecological equivalent of *Sus scrofa* in the Old World (Lundelius, 1960:34). Morphologically, however, *Platygonus* is a better candidate. Note that in limb proportions (tables 5 and 6) *Platygonus* and *Sus* appear to be similar: Both are longer-limbed than modern forest forms.

The loss of the external "dew claws" in *Platygonus*, leaving only vestigial bone splints to represent metacarpals II and V and metatarsal II is, so far as known, unique among tayassuids, living or extinct. All the lateral metapodials of *Platygonus* are reduced to the same relative size as that of metatarsal V of the two living species of peccary, leaving no external indication of their presence. This structural change apparently predated the Wisconsinan glaciation, as it is characteristic of *P. cumberlandensis* from Cumberland Cave, Maryland, as well as of *P. compressus*.

TABLE 5. RELATIVE LIMB PROPORTIONS AND MEASUREMENTS (IN MM.), TAYASSUIDAE

Skeletal element	<i>Tayassu pecari</i> AMNH 80010	<i>Tayassu tajacu</i> G-823	<i>Platygonus compressus</i> Paducah #1*	<i>Mylohyus nasutus</i> TMM 933-3232**
<u>radius</u>	72%	69%	78%	84%
humerus	(119/166)	(95.6/138)	(160/206)	(182/217)
<u>metacarpal IV</u>	38%	36%	45%	47%
humerus	(63.3/166)	(49/138)	(92.1/206)	(103/217)
<u>tibia</u>	94%	94%	99%	105%
femur	(161/172)	(135/144)	(198/201)	(230/216)
<u>metatarsal IV</u>	—	41%	46%	53%
femur		(59/144)	(92.4/201)	(115/216)

\*Unpublished data from Whitmore (National Museum of Natural History).

\*\*Data from Lundelius, 1960.

Measurements in parentheses.

TABLE 6. RELATIVE LIMB PROPORTIONS AND MEASUREMENTS (IN MM.), SUIDAE.

Skeletal element	Giant Forest Hog <i>Hylochoerus</i> <i>meinertzhageni</i> MCZ 27851	Bush-Pig <i>Potamochoerus</i> <i>porcus</i> MCZ 5151	Wild Boar <i>Sus scrofa</i> MCZ 51621	Warthog <i>Phacochoerus</i> <i>aethiopicus</i> MCZ 5009 (immature)
<u>radius</u>	71%	75%	75%	74%
humerus	(191/268)	(137/182)	(177/235)	(115/155)
<u>metacarpal IV</u>	30%	36%	38%	46%
humerus	(80/268)	(66/182)	(89/235)	(71/155)
<u>tibia</u>	79%	89%	91%	97%
femur	(221/279)	(172/194)	(227/249)	(159/164)
<u>metatarsal IV</u>	30%	39%	42%	48%
femur	(83/279)	(75/194)	(105/249)	(79/164)

Measurements in parentheses.

TABLE 7. RATIO, DEPTH OF ZYGOMATIC ARCH TO DIAMETER OF ORBIT,  
*Platygonus compressus*

Diameter of Orbit in mm.	Depth of Zygomatic Arch in mm.	Dental Age*	100 X <u>Zygomatic depth</u> Eye Diameter	Catalog Number
31.8	37.4	6	118	CM 12650
32.4	41.4	7	128	AMNH 45703
33.0	27.0	5	82	CM 12642
33.9	31.5	6	93	CM 12885
34.5	33.3	4	96	AMNH 45702
34.7	35.4	6	98	CM 12886
34.8	41.5	6	119	CM 12641
35.0	35.3	4	102	CM 12888
35.1	38.7	7	110	CM 12887
35.3	35.4	4	100	CM 12649
35.5	33.4	7	94	AMNH 45705
36.0	31.1	6	86	CM 12657
36.4	37.7	8	102	AMNH 45701
36.4	37.7	6	103	CM 12630
37.0	31.0	4	84	CM 2806

No apparent correlation in depth of zygomatic flange with dental age or individual size (as evidenced by diameter of orbit).

\*Defined in text.

Various localities represented.

TABLE 8. SKELETAL MEASUREMENTS (IN MM.), *Platygonus compressus*,  
WELSH CAVE, KENTUCKY

Measurement	$\bar{X}$	S.D.	V	O.R.	N
Skull					
Greatest length	306.5	8.12	2.64	293-318	11
Condylobasal length	278.2	8.16	2.93	265-291	11
Anterior margin of foramen magnum to anterior of premaxilla	266.2	11.90	4.48	252-287	8
Anterior border of orbit to anterior of premaxilla	191.6	6.88	3.58	184-202	5
Zygomatic breadth	130.4	8.20	6.28	121-143	7
Breadth of skull above P <sup>2</sup>	42.0	3.68	8.74	36.2-46.2	8
Depth of zygoma: end of postorbital process to end of preglenoid process	65.8	5.50	8.42	57.2-75.3	13
Depth of zygoma: middle below orbit	36.7	3.04	8.28	31.1-41.5	14
Vertical diameter of orbit	34.9	1.69	4.84	31.8-39.0	13
Width across canines: all specimens	65.5	6.98	10.65	57.4-85.0	12
Width across canines: suspected male omitted, see text	63.7	3.46	5.43	57.4-69.6	11
Height of canine buttress from alveolus: all specimens	34.6	4.25	12.26	30.2-46.9	13
Height of canine buttress from alveolus: suspected male omitted, see text	33.6	2.23	6.62	30.2-37.5	12
Palatal width, between canines	40.32	3.01	7.46	36.1-47.4	13
Palatal width, just anterior to P <sup>2</sup>	31.1	2.38	7.66	28.3-36.4	15
Palatal width, between P <sup>2</sup> 's	24.4	1.65	6.74	21.6-27.5	18
Palatal width, between M <sup>2</sup> 's	23.2	2.46	10.60	19.0-29.3	18
Length of upper pre-canine diastema	21.2	1.53	7.20	18.6-23.2	13
Length of upper post-canine diastema	45.1	1.73	3.80	42.6-47.5	15
Height of occiput from ventral border of condyles	94.9	5.31	5.59	85.7-106.6	17
Width of, and including, occipital condyles	50.99	3.20	6.26	45.7-59.7	23
Mandible					
Total length	218.1	5.96	2.73	210-230	12
Height	94.6	4.99	5.27	87.1-103.0	10
Length, post-canine diastema	51.5	3.50	6.80	48.0-61.7	18
Least depth below post-canine diastema	31.2	1.53	4.91	28.4-34.4	18
Depth below anterior margin of M <sub>1</sub>	39.0	2.70	6.93	32.7-43.3	18
Length of symphysis	70.5	3.06	4.34	67.2-77.9	15



TABLE 8. SKELETAL MEASUREMENTS (IN MM.), *Platygonus compressus* (continued)

Measurement	$\bar{X}$	S.D.	V	O.R.	N
Deciduous dentition					
Length dP <sup>2-4</sup>	32.2	.88	2.74	30.9-33.3	6
Length dP <sup>4</sup>	12.2	.52	4.24	11.2-12.8	11
Width dP <sup>4</sup>	11.3	.49	4.32	10.3-12.1	13
Length dP <sub>2-4</sub>	34.7	—	—	33.1-37.8	4
Length dP <sub>4</sub>	16.6	.61	3.66	15.9-17.5	17
Width dP <sub>4</sub>	8.6	.50	5.83	7.8-9.7	17
Permanent dentition					
Length P <sup>2</sup> -M <sup>3</sup>	75.7	2.79	3.68	70.2-80.1	12
Length P <sup>2</sup> -P <sup>4</sup>	28.1	1.22	4.35	25.4-29.5	12
Length M <sup>1</sup> -M <sup>3</sup>	47.9	1.75	3.66	44.5-50.4	14
Upper canine, antero-posterior diameter	15.0	1.45	9.65	13.2-17.2	22
Upper canine, transverse diameter	8.4	.84	10.15	7.1-9.7	22
P <sup>2</sup> , length	8.7	.49	5.70	7.8-9.3	13
P <sup>2</sup> , width	9.1	.50	5.53	8.1-9.9	13
P <sup>3</sup> , length	9.9	.48	4.83	9.0-10.8	18
P <sup>3</sup> , width	11.0	.58	5.32	10.1-12.3	19
P <sup>4</sup> , length	9.8	.42	4.34	9.0-10.4	17
P <sup>4</sup> , width	12.2	.57	4.63	11.2-13.4	17
M <sup>1</sup> , length	12.9	.60	4.66	11.9-14.1	17
M <sup>1</sup> , width	12.6	.38	3.00	12.2-13.6	17
M <sup>2</sup> , length	16.2	.57	3.49	15.4-17.5	17
M <sup>2</sup> , width	15.0	.56	3.70	14.1-16.1	17
M <sup>3</sup> , length	18.4	1.39	7.54	16.7-21.4	16
M <sup>3</sup> , width	15.2	.68	4.49	13.9-16.1	16
P <sub>2</sub> -M <sub>3</sub> , length	78.0	2.59	3.32	73.9-80.6	5
P <sub>2</sub> -P <sub>4</sub> , length	28.7	.49	1.73	28.0-29.2	5
M <sub>1</sub> -M <sub>3</sub> , length	50.1	1.95	3.90	45.3-53.0	16
Lower canine, antero-posterior diameter	11.7	.86	7.38	10.5-13.2	19
Lower canine, transverse diameter	8.7	.64	7.38	7.8-10.1	18
P <sub>2</sub> , length	8.1	.45	5.60	7.4-8.5	5
P <sub>2</sub> , width	6.4	.35	5.52	6.0-6.9	5
P <sub>3</sub> , length	10.2	.48	4.76	9.2-10.8	15
P <sub>3</sub> , width	7.9	.49	6.22	7.3-8.6	15
P <sub>4</sub> , length	10.8	.65	6.06	9.5-11.9	16
P <sub>4</sub> , width	9.4	.62	6.59	7.8-10.3	16
M <sub>1</sub> , length	13.6	.73	5.37	12.5-15.3	25
M <sub>1</sub> , width	9.9	.54	5.44	9.1-11.3	25
M <sub>2</sub> , length	15.9	.63	3.96	15.0-17.5	30
M <sub>2</sub> , width	12.2	.71	5.84	10.9-14.0	30
M <sub>3</sub> , length	21.4	1.00	4.68	19.4-23.0	22
M <sub>3</sub> , width	12.5	.75	6.01	11.5-13.7	22

TABLE 8. SKELETAL MEASUREMENTS (IN MM.), *Platygonus compressus* (continued)

Measurement	$\bar{X}$	S.D.	V	O.R.	N
Postcranial Measurements					
Greatest width of atlas	98.7	4.50	4.60	92.0-106.0	8
Width of condylar facets of atlas	51.6	2.40	4.77	48.3-55.3	17
Length of sacrum	112.2	10.40	9.20	98.7-123.0	8
Width of centrum of sacrum	34.0	2.73	8.03	31.0-40.3	17
Antero-posterior diameter, neck of scapula	22.7	1.86	8.10	19.2-26.6	35
Length of humerus	190.1	6.20	3.20	181-201	22
Maximum distal width of humerus	40.7	1.80	4.64	38.0-44.5	32
Length of radius	157.0	6.50	4.10	141.0-166.0	15
Proximal width of radius	30.3	1.60	5.30	27.7-33.6	28
Length of ulna	206.9	5.10	2.40	198.0-214.0	12
Antero-posterior diameter, olecranon process of ulna	28.8	1.80	6.20	26.7-33.3	27
Distal width, fused radius & ulna	40.7	1.90	4.70	37.2-44.9	26
Least width of ilium, long diameter	35.0	3.50	10.06	29.4-41.0	17
Length of femur	187.3	6.60	3.52	179.0-200.0	19
Least shaft width of femur	19.6	1.08	5.49	17.9-22.2	23
Distal width of femur	45.3	2.33	5.15	41.7-50.3	31
Length of tibia	194.2	7.15	3.68	184.0-207.0	15
Proximal width of tibia	47.8	1.50	3.20	45.0-51.0	15
Distal width of tibia	29.9	1.53	5.11	27.3-33.2	17
Length metacarpal III (from articular surface)	85.5	2.93	3.42	81.1-92.7	24
Length metacarpal IV (from articular surface)	86.3	3.14	3.63	82.0-91.3	28
Length of metatarsal	91.1	2.49	2.74	86.6-96.6	29
Length of astragalus	39.8	1.91	4.79	37.4-43.7	25
Length of calcaneum	71.8	2.73	3.80	65.3-76.4	24
Width across sustentaculum of calcaneum	31.6	1.49	4.72	28.4-33.8	32
Length of proximal phalanx I	38.4	1.55	4.04	34.5-41.2	79
Length of middle phalanx II	29.0	1.20	4.28	26.0-31.3	69
Length of distal phalanx III	30.6	2.09	6.83	26.4-34.1	53
Length of patella	34.7	2.04	5.90	30.8-37.7	18

This apparently unique suppression of the six external dew claws that are "normal" in tayassuids may be of little value in tracing the evolutionary history of the genus, however. In the Bovidae dew claws may be present or absent in genera that otherwise appear closely related, e.g., the antelopes *Nesotragus* and *Neotragus*. The mutation in *Platygonus* may have been comparable to such aberrations as the vertebral interdigitations of *Scutisorex* and the anomalous dentition of *Otocyon*, as far as its taxonomic value is concerned.

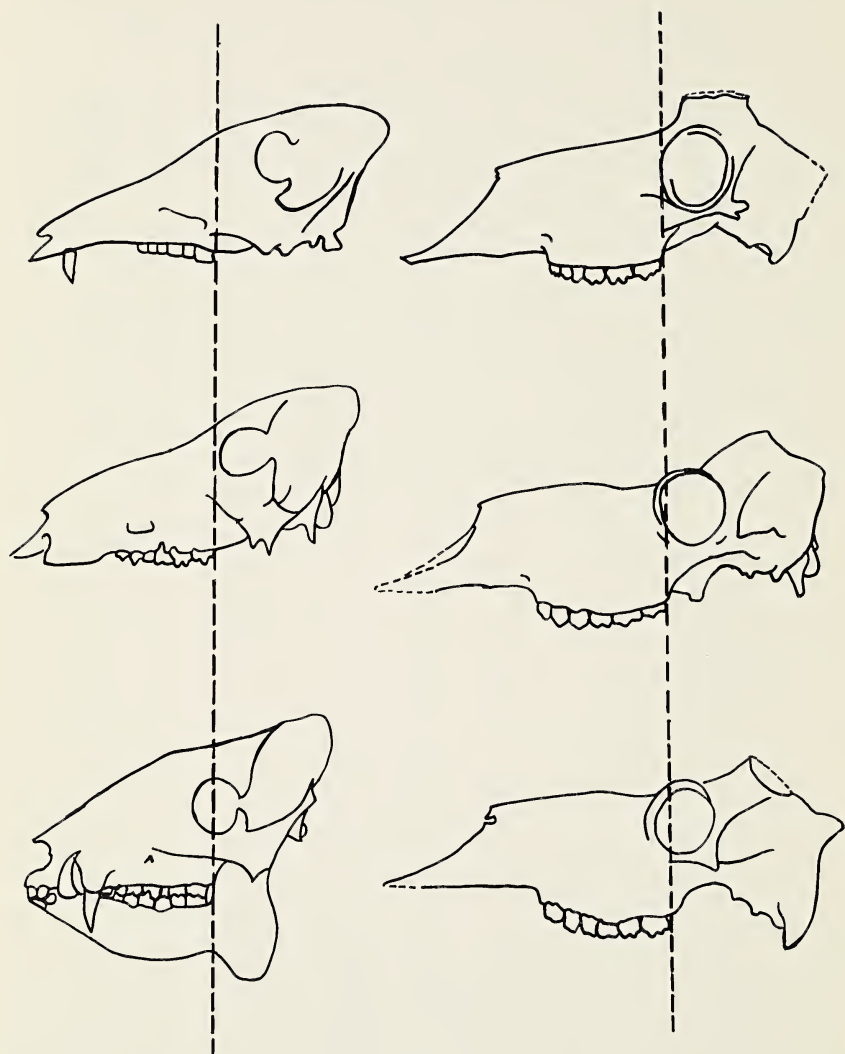


Fig. 18. Position of eye socket in relation to last upper molar in various Artiodactyla, correlated with habitat preference. See also fig. 19.

*Mylohyus nasutus*, extinct, habitat?

*Platygonus compressus*, extinct, habitat?

*Tayassu tajacu*, open woodlands, brush desert, rain forest.

*Antilocapra americana*, plains.

*Rangifer tarandus*, open woodland, tundra.

*Odocoileus virginianus*, woodlands, forest edge.

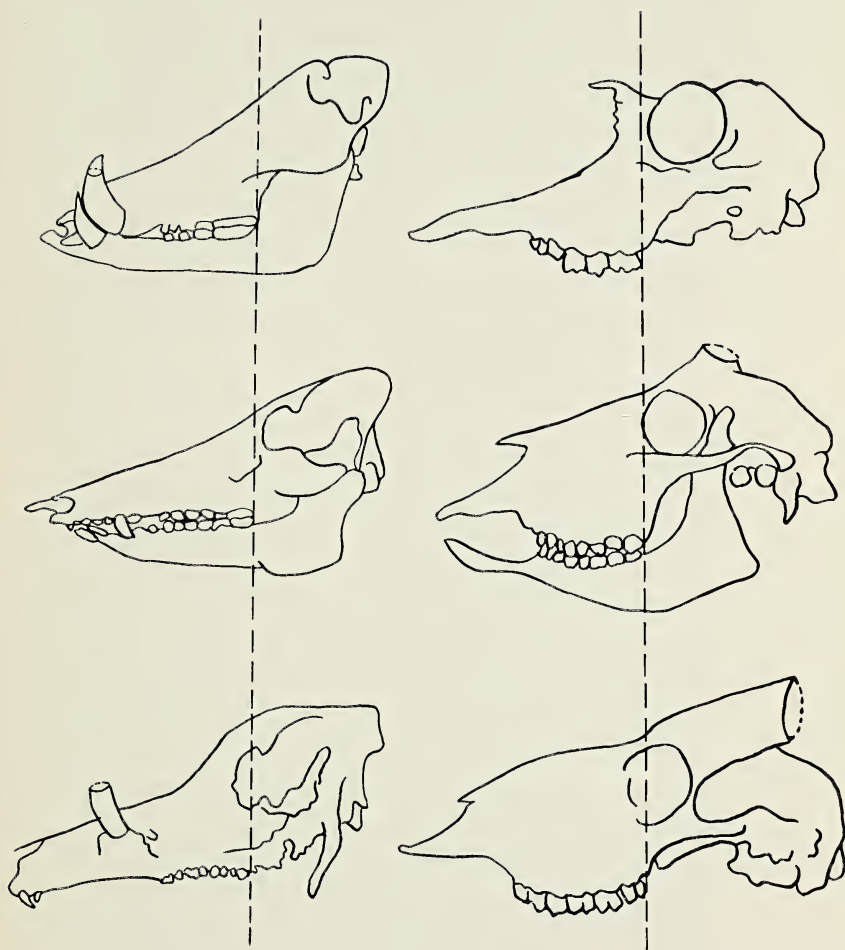


Fig. 19. Position of eye socket in relation to last upper molar in various Artiodactyla, correlated with habitat preference. See also fig. 18.

*Phacochoerus aethiopicus*, tropical savannah.

*Sus scrofa*, woodland, forest edge.

*Babyrousa babyrussa*, tropical forest.

*Saiga tatarica*, plains.

*Procapra gutturosa*, plains.

*Boocercus eurycerus*, tropical forest.





Fig. 20. X-ray positive. Skulls of *Platygonus compressus*, Welsh Cave, Kentucky (left) and *Tayassu tajacu* (right), frontal views. Note relative position of eye sockets.

Several modifications of the skull appear to accompany these cursorial adaptations. In both modern species of peccary (fig. 18) a line erected vertically from the back of the upper tooth-row intersects the orbit at about mid-point. In *Platygonus* and also in the long-nosed peccary, *Mylohyus*, the eye lies to the rear of such a line. It is obvious, as pointed out by Leidy (1889:42), that the orbit of *Platygonus*, compared with that of *Tayassu*, has migrated caudally and is situated higher and more laterally in the cranium (fig. 20). Several modern parallels among the artiodactyls, seemingly correlated with habitat, suggest themselves. Figures 18 and 19 illustrate relative positions of eye orbit that appear to correlate with varying degrees of preference for open country in living mammals. This position of the orbit with relation to the maxillary tooth-row may also be followed in the evolution of the Equidae, and would appear to be, at least in part, a modification associated with greater dependence on eyesight. The lateral position of the eyes of *Platygonus* in comparison with that of *Tayassu* may be readily seen in figures 20 and 21. It is also apparent in such artiodactyls as *Antilocapra*, as opposed to *Odocoileus*; *Giraffa*, as opposed to *Okapia*; *Pantholops*, as opposed to *Boocercus*. The lateral position of the eye, apparently again associated with habitat, may also be seen in lagomorphs. In this group, increasing degree of lateral placement is reflected in the development of the supra-orbital flange that overhangs the orbits, affording protection for the eye.

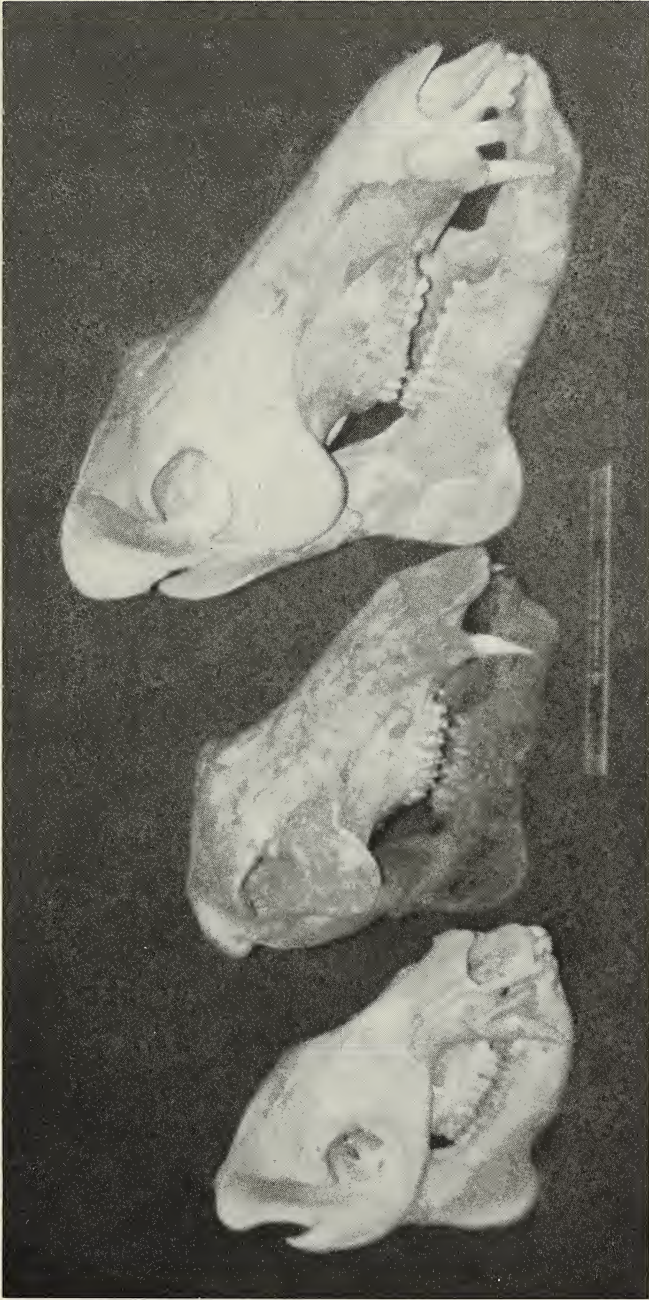


Fig. 21. Oblique view, crania. Left: *Tayassu tajacu*, G-8250. Center: *Platygonus compressus*, CM 12641. Right: *Platygonus cumberlandensis*, NMNH 8150 (rostrum restored). Lower jaws of CM 12641 and NMNH 8150 not found associated with crania. Note relative development of zygomatic flare and relative sizes.

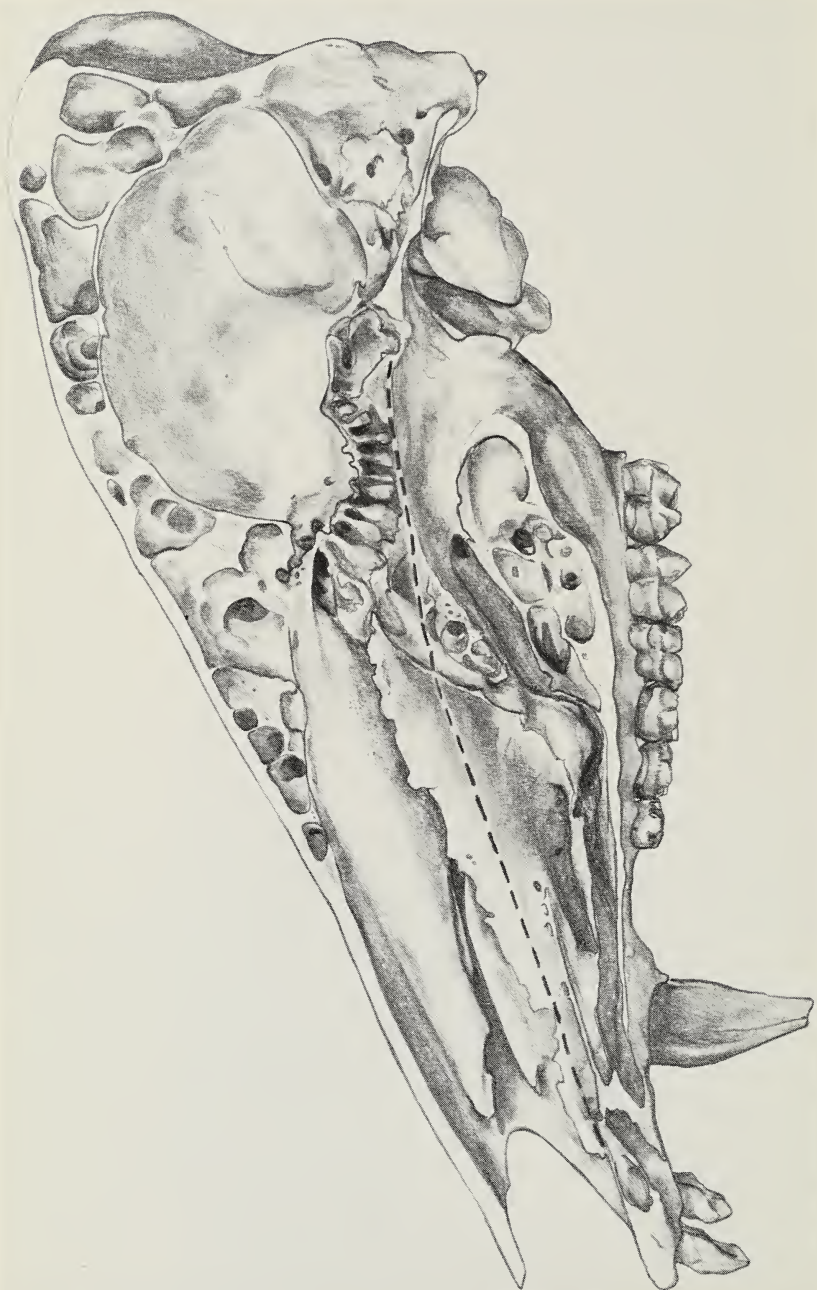


Fig. 22. *Tayassu pecari*, cranium, AMNH 80010, Recent, sagittal section.



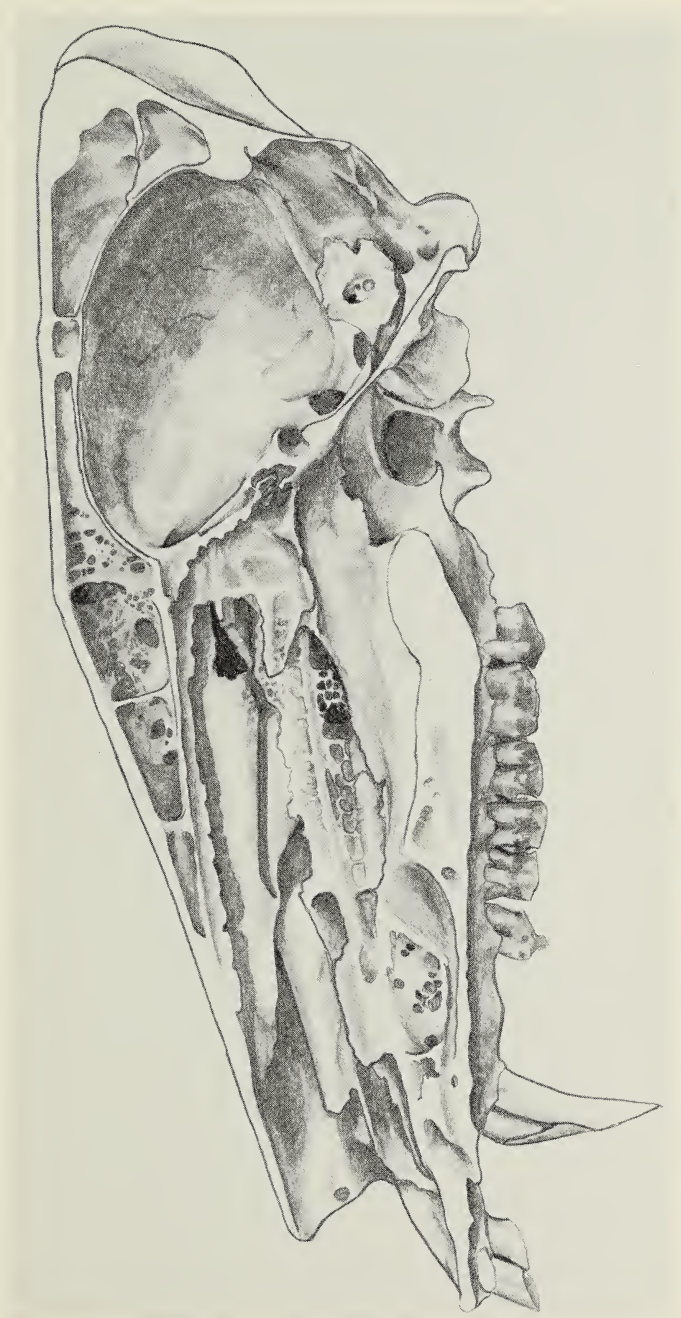


Fig. 23. *Tayassu tajacu*, cranium, G-823, Recent, sagittal section (negative reversed).



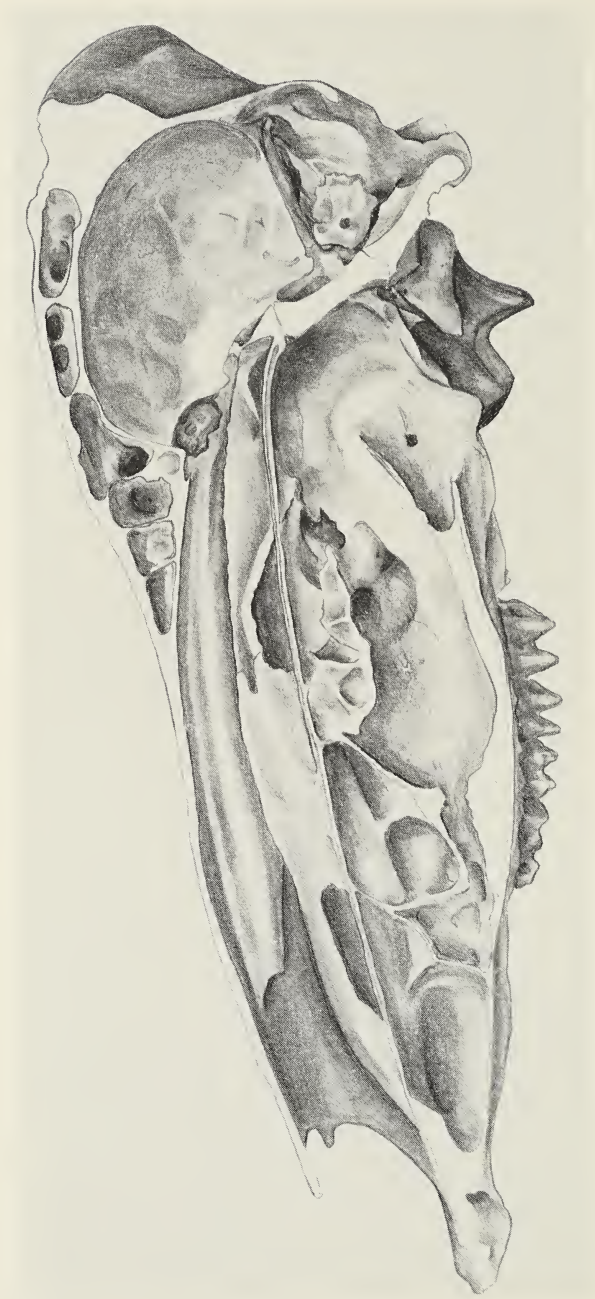


Fig. 24. *Platygonus compressus*, cranium, CM 12888, late Pleistocene, Welsh Cave, Kentucky, sagittal section.

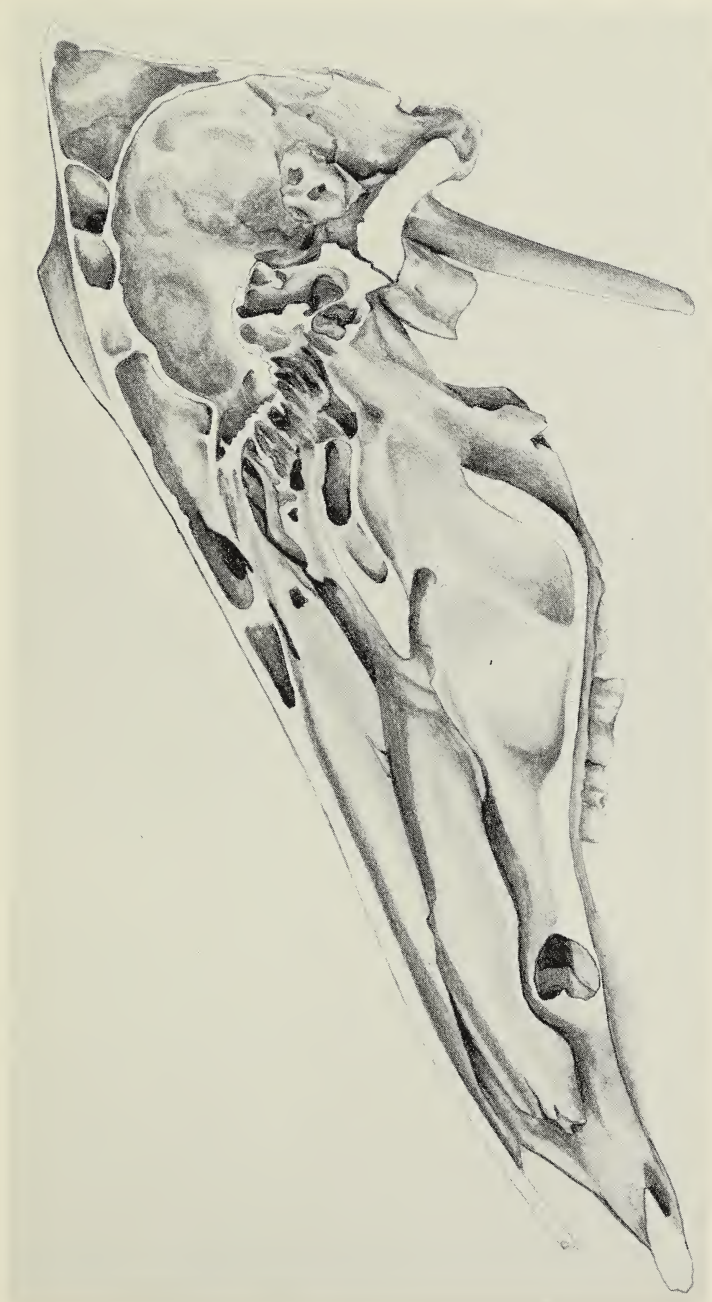


Fig. 25. *Phacochoerus aethiopicus*, cranium, G-829, Recent, Rhodesia, sagittal section.

A progression is noticeable in a sequence starting with *Romerolagus diazi*, a skulking form of almost microtine habitus in which the supra-orbital flange is barely suggested, to its greater development in *Sylvilagus*, a wood and field-edge form, to still greater development in the snowshoe hare, *Lepus americanus*, a coniferous-forest, muskeg, and taiga form, reaching its greatest development in the large open-country jackrabbits like *Lepus californicus*.

In the case of *Platygonus* it is a moot question whether this shift of the eye to the rear is just that or rather a lengthening of the preorbital half of the skull. The glenoid fossa appears to remain in the same position with relation to the teeth (fig. 18) as in *Tayassu*. The mandibular association is roughly the same in both forms.

A bending of the basiocranial axis of the skull appears to be associated with this eye positioning (compare figs. 22, 23, 24, and 25), a modification enabling the eye to remain in a more horizontal relationship while the animal is in a grazing attitude. This, as well as the modified eye position, is also characteristic of the African warthog, *Potamochoerus*, as opposed to other suids (fig. 25).

Figures 22, 23, and 24, represent sectioned skulls of *Tayassu pecari*, *Tayassu tajacu*, and *Platygonus compressus*, respectively, reduced to the same relative size. Several distinctions can be made. The most obvious are the relatively smaller size of the brain cavity and the much greater degree of development of the olfactory areas and paranasal sinuses of *Platygonus*, first pointed out by Leidy, 1853. Note the greater thickness of the basisphenoid and the basioccipital in *Platygonus*, suggesting stronger attachment for the cranial flexors, also the smaller auditory bullae and the relatively smaller *petrous temporal*.

The relationship of the *masseter lateralis* muscle to the skull and the mandibles differs slightly between *Tayassu* and *Platygonus*. In both species of *Tayassu* it originates along the zygomatic arch at approximately the same level as the glenoid fossa and roughly parallel with the tooth-row. It extends from a point above  $M^1$  posteriorly to the glenoid fossa (Woodburne, 1968:12 and fig. 9). The area of insertion on the mandible subtends an arc of  $30^\circ$  anterior and  $25^\circ$  posterior to a perpendicular extended through the condyles. The angle formed at the glenoid fossa by the line of origin and the posterior line of insertion of *masseter lateralis* is about  $110^\circ$ . The pull of the entire muscle mass is inclined forward at an angle of about  $30^\circ$  from the perpendicular. In *Platygonus*, however, the area of insertion of *masseter lateralis* is at a greater angle to



the tooth-row, and does not extend as far forward on the skull. It rises sharply anterodorsally at about a  $30^\circ$  angle and extends much farther posteriorly in relation to the molars (figs. 18 and 21). The insertion scar is much more pronounced and about a third longer in *Platygonus* (CM 12624) than in the skull of *T. pecari* (AMNH 80010) of comparable size. Just as the origin of *M. m. lateralis* has shifted posteriorly (in relation to both the molar row and to its position in *Tayassu*), so has the area of insertion on the mandible shifted forward. It subtends an arc of approximately  $55^\circ$  along the gonial ridge anterior to a perpendicular dropped from the condyle, about  $15^\circ$  more than in *Tayassu*, and extends posteriorly along the gonial ridge to a point just slightly behind that perpendicular, rather than  $25^\circ$  behind, as in *Tayassu*. As in *Tayassu* the angle formed between the line of origin and the condyle, and the posterior point of insertion and the condyle is about  $120^\circ$ . However, unlike *Tayassu*, the major axis of contraction of the muscle appears to have been straight up and down, at right angles to the load applied on the teeth during mastication, rather than obliquely forward as in *Tayassu*. This increases the efficiency of the jaw apparatus by preventing any waste motion anteroposteriorly. It also increases the relative power of the muscle by shifting the axis of contraction higher in relation to the tooth-row. This might be envisioned as the capability to drive the lower jaw right through the upper, and is expressed in greatly increased chewing power. In some suids, *Phacochoerus*, for example, as opposed to *Sus*, the same result is obtained by raising the glenoid fossa in relation to the tooth-row, thus increasing the relative length of the ascending ramus.

Both the internal and external pterygoid muscles were more highly developed in *Platygonus* than in either of the two modern species of *Tayassu*. This, plus the relatively smaller paraoccipital process, indicating a smaller *digastricus* muscle, and the extreme hypsodonty of the bilophodont molars, limiting any anteroposterior movement during occlusion, indicates an orthal chewing cycle.

The dentition of *Platygonus*, compared with the living peccaries, is specialized. The incisors and canines are more gracile in appearance.  $I^2$ , well developed in modern peccaries, is reduced to a small peg, and  $I_3$  has been lost altogether. In this respect *Platygonus* again appears more specialized than the two living species, yet less so than in *Mylohyus*, where reduction of incisors and canines is carried even further (fig. 26). The cheek dentition (fig. 27) is hypsodont and functionally lophodont, strikingly different from *Mylohyus* or modern *Tayassu*, in which the





Fig. 26: Canines and incisors, various tayassuidae.

Row A: Recent *Tayassu tajacu*, G-825.

Row B: late Pleistocene *Platygonus compressus*, CM 2806.

Row C: Recent *Tayassu pecari*, AMNH 80010.

Row D: D-1 milk dentitions, *Mylohyus nasutus*, CM 8560 late Pleistocene (left); *Tayassu tajacu*, G-824 Recent (right); D-2 *Mylohyus nasutus*, TMM 933-3232, late Pleistocene; D-3 *Mylohyus nasutus*, late Pleistocene (Parmalee, *et al.*, 1969).

Column 1: Upper incisors and canines, crown view.

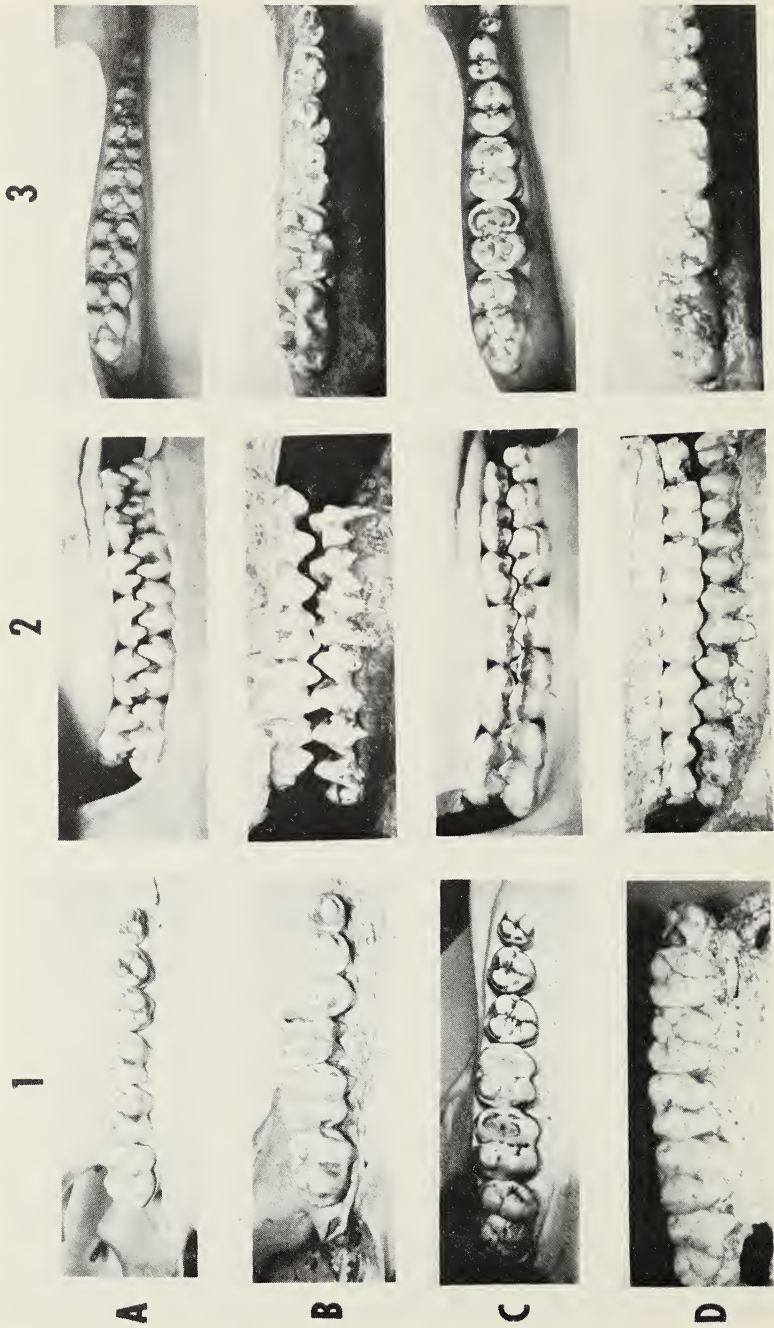
Column 2: Incisors and canines, side view.

Column 3: Lower incisors and canines, crown view.

molars and premolars are more bunodont. Premolars of *Platygonus* are not molariform, but form a highly efficient lophodont battery. Dentitions of the two modern peccaries are more conservative. The cheek series of *T. pecari* is somewhat more bunodont than *T. tajacu*, but both lie intermediate in appearance between the extremes exhibited by *Platygonus* on one hand and *Mylohyus* on the other. The dentition of *Platygonus* would seem to be adapted to browsing, much more so than in the Old World *Sus*, although it is still essentially that of a modified omnivore.

In summary, compared with the two modern species of peccary (primarily tropical woodland or, at best, marginally open-country forms), *Platygonus* appears to possess a constellation of characters that one might expect from an open country form: greater size (fig. 28); increased length of limbs; greater dependence upon eyesight and smell, as suggested by the migration of the eye and the hypertrophy of the nasal organs; a dentition more suggestive of a browsing herbivore than of an omnivore; a change in the angle of the basicranial axis; and a thickening of the basilar tubercles indicating a much greater development of *M. longus capitis*, suggestive of grazing or browsing movements of the head. It is not surprising that the two living peccaries should exhibit a greater degree of conservatism in structure than the two now extinct genera. An increase in specialization is always accompanied by a decrease in adaptability. The anatomy of *Platygonus* suggests that it was adapted for something other than dense forest and was more of a browser than either modern species.

**TAXONOMIC NOTES:** As with most large Pleistocene mammals, many species of *Platygonus* have been described. Museum collections of this genus are now becoming so common that it may soon be possible to review it profitably. In the Appalachian area of north-central and north-eastern North America, the area most familiar to us, there appear to have been but two species—the smaller Wisconsinan and post-Wisconsinan form, *Platygonus compressus* LeConte, comprising approximately 90% of the reported finds, and the larger *Platygonus cumberlandensis* (probably including *P. intermedius* and *P. vetus*). Judging from the accompanying fauna, *P. cumberlandensis* is pre-Wisconsinan and probably Illinoian in age. Other referred specimens are probably pre-Wisconsinan as well. Figures 21 and 30 illustrate the cranial distinctions that separate the two species: the greater size of *P. cumberlandensis*, somewhat longer rostrum, and greater development of suborbital zygomatic flare and nuchal crest. Since the major distinction between the pre-Wisconsinan





form and the post-Wisconsinan form is size and its attendant rugosity, the interpretation of some population samples is equivocal. For instance, the Laubach Cave population appears to be intermediate in size between *P. cumberlandensis* and *P. compressus*. It is also farther south than other major samples. If, as appears probable, at least, *P. compressus* and *P. cumberlandensis* represent points along a temporal size cline, how can intermediate specimens be interpreted? As intermediate in age? Or perhaps *Platygonus* exhibited a geographically (hence climatically) dictated size cline. Such intermediate finds, on the basis of size characteristics alone, could not be assigned a temporal position due to suspected geographic variation, or regarded as indicators of varying degrees of climatic stress due to a possible temporal cline. Questions like these must be left to future research, but the genus *Platygonus* does appear to offer insights that could be derived from few other North American Pleistocene forms because of its widespread distribution and its frequency in museum collections.

**EXTINCTION:** The enigmatic question arises, of course. Why are these animals extinct? Widespread geographically, and apparently quite common, they survived well into post-glacial times, but appear to have been victims of the same circumstance or circumstances that eliminated so many large mammals from the world during that time span. They appear to have had habits somewhat similar to the wild boar of Europe, which still survives. Much of the area over which *Platygonus* once ranged is now occupied by feral *Sus scrofa*. In fact, some of the former range of *Platygonus* is now occupied by *Tayassu* in the American Southwest. It is interesting to note that *Tayassu*, however, does not occur in Pleistocene or early post-Pleistocene deposits that contain *Platygonus* (Lundelius, 1967). *Tayassu* apparently spread north to occupy and exploit former *Platygonus* territory, implying, in the light of the marked

◀  
Fig. 27. Dentitions of Recent and Pleistocene peccaries, anterior to the right.

Row A: *Tayassu tajacu*, CM 672, Recent.

Row B: *Platygonus compressus*, CM 21624, CM 12632, CM 12636, Pleistocene, Welsh Cave, Kentucky.

Row C: *Tayassu pecari*, AMNH 80010, Recent.

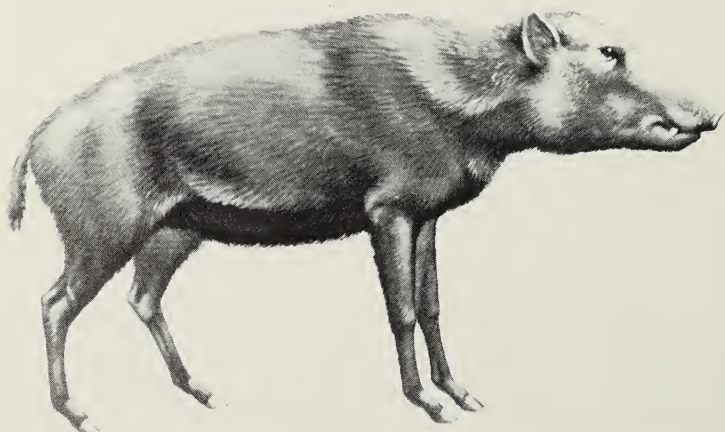
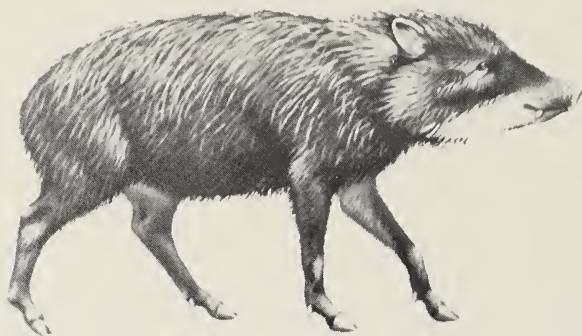
Row D: *Mylohyus nasutus*, Pleistocene, CM 12609, Organ-Hedricks Cave, West Virginia (upper dentition); CM 2330, Frankstown Cave, Pennsylvania (lower dentition).

Column 1: Right upper dentitions, crown view.

Column 2: Right dentitions in occlusion, buccal view.

Column 3: Right lower dentitions, crown view.





anatomical differences between the two genera, environmental changes at least marginally favorable for *Tayassu*, but fatal for *Platygonus*.

Suids and tayassuids differ markedly in their breeding capacity. *Tayassu tajacu* usually has a litter size of two, but occasionally three, with a gestation period of five months (Sowls, 1966), while *Sus scrofa* in the wild produces four to six young with a shorter gestation period of slightly less than four months. If the extinct peccaries, *Platygonus* and *Mylohyus*, were also relatively slow breeders, this, coupled with their obvious specialization away from an omnivorous mode of life, may explain why they were unable to cope with environmental changes that wiped them out both in temperate North and South America, while the Old World pigs were unaffected by late Pleistocene changes. There is no evidence that man played a part in the extinction of these animals. Their geographic range was so huge that more than local hunting pressure would seem to be called for. We suggest that the environmental niche to which they were adapted either vanished or diminished because of post-Wisconsinan climatic change, automatically reducing numbers, thus allowing other pressures like direct competition (perhaps by bears?) and predation to be more effective in reducing numbers still further. Finally, reproduction could no longer keep pace with environmental attrition.

#### FAUNAL ANALYSIS

There were 27 mammals represented in the Welsh Cave local fauna, possibly a third of the total fauna of depositional times. While there is some evidence of secondary deposition, all species, with the exception of the opossum (*Didelphis marsupialis*), appear to be contemporaneous, or at least are found intermingled with peccary and dire wolf remains. We shall consider them as contemporaries, with the exception of the opossum, which has been omitted from the faunal list.

The recovered fauna, therefore, consists of four insectivores, 11 rodents, four carnivores, one elephant, one horse and one peccary. Fragmentary box turtle (*Terrapene*, ?species) carapace fragments recovered from the surface talus are considered Recent contamination. Some land snails were also present.



Fig 28. Various peccaries drawn to same relative scale by wildlife artist Charles L. Ripper. Top: modern collared peccary, *Tayassu tajacu*; center: modern white-lipped peccary, *Tayassu pecari*; bottom: extinct flat-headed peccary, *Platygonus compressus*. Restoration based upon Welsh Cave specimens. Note greater relative length of limbs and rostrum, position of eye, and absence of dew claws in *Platygonus compressus*.

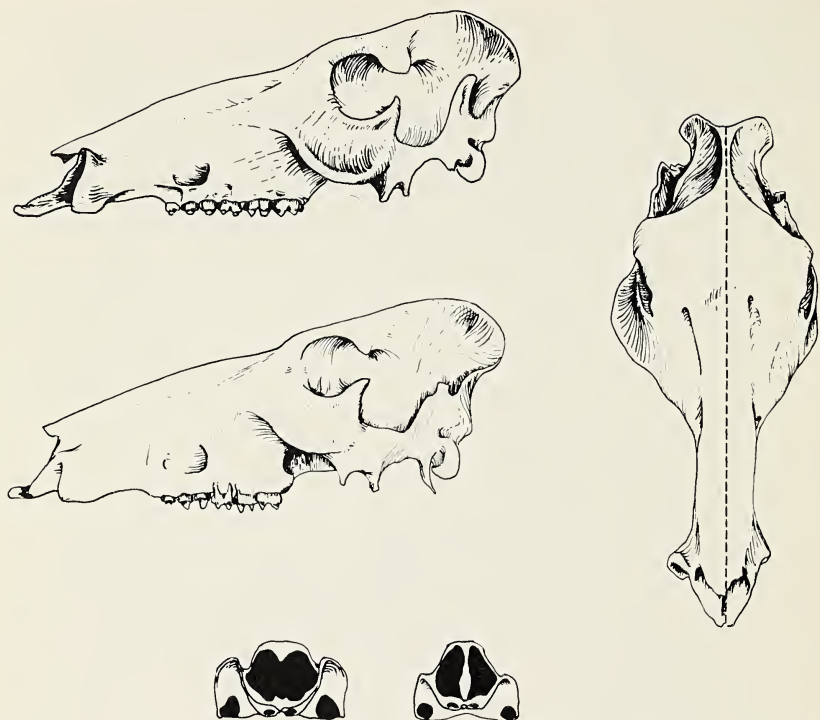


Fig. 29. Extremes in development of zygomatic flare and canine buttress, *Platygonus compressus*, Welsh Cave, Kentucky. CM 12650 (top); CM 12624 (center). Right: dorsal view of same crania abutting along mid-line. Bottom: anterior view of premaxilla, canine buttresses, and external nares (left, CM 12650; right, CM 12624).

Utilizing the carbon-14 date derived from the collagen content of the peccary bones— $12,950 \pm 950$  B.P. (I-2982), the Welsh Cave local fauna accumulated in post-Cary times at about the time of the Port Huron (Mankato) substage. The Huron icelobe was approximately 350 miles north of the cave entrance and was fronted along its southern edge by glacial Lake Whittlesey approximately 250 miles north of the cave (Wayne and Zumberge, 1965:63-84). The fauna appears to be consistent with the concept of boreal woodland.

The species recovered from Welsh Cave can be divided into several groups on the basis of their present distribution. *Platygonus*, *Canis dirus*, *Mammuthus* sp., and *Equus* sp. are extinct and supply no direct ecological information. *Ursus arctos*, *Taxidea*, *Spermophilus tridecemlinea-*



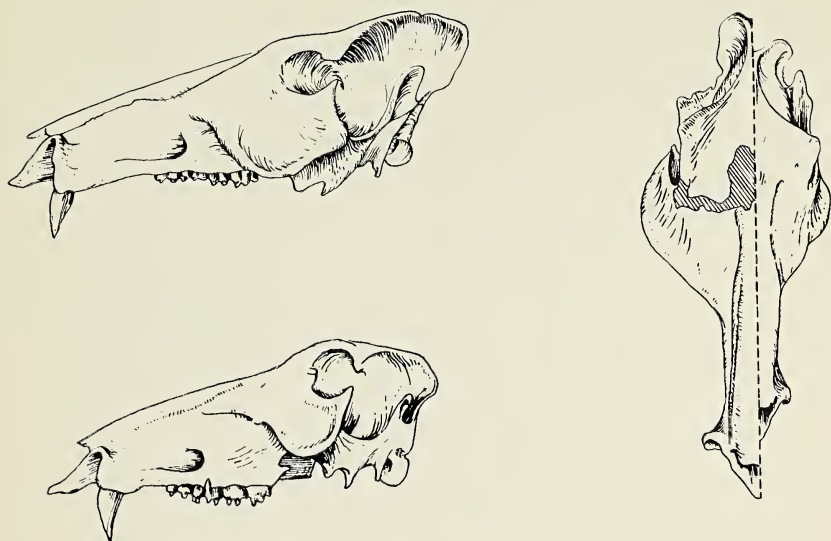


Fig. 30. *Platygonus cumberlandensis*, NMNH 8146, Cumberland Cave, Maryland (above), and *Platygonus compressus*, CM 12641, Welsh Cave, Kentucky (below). Molars to same scale. Left: lateral views. Right: dorsal views abutting along midline. Note flare and depth of zygoma, development of nuchal crest, and diastema of skulls.

*tus*, and in all probability, *Geomys* (see discussion under Geomyidae, "Species Notes"), form a distinct western element. None of them occur today east of the Mississippi River except in the "prairie peninsula" region north of the Ohio River in the Illinois-Indiana area. Their presence in the fauna would seem to call for tracts of open country. This hypothesis is reinforced by the low numbers of woodland animals, like tree squirrels, in the fauna.

By far the commonest small mammal in the deposit, the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), is not a member of the Recent fauna and is rigidly restricted to open prairie or prairie enclaves today. This is the first record for the species from Kentucky. It has been recorded from Pleistocene sites as far south as Robinson Cave, north-central Tennessee, and is a common species in late Pleistocene boreal faunas from the mid-Appalachians (Guilday, in press). The common ground squirrel of the area today, the chipmunk (*Tamias striatus*), is not represented in the fauna despite the commonness of the prairie ground squirrel, suggesting a relative lack of brushy forest cover.



The thirteen-lined ground squirrel is very sensitive to ground cover. A colony at Polk, northwestern Pennsylvania (Richmond and Rosland, 1949) accidentally established by escaped animals some 70 years ago, is restricted to pasture fields, cemeteries, and churchyards within a few miles of Polk, and has not spread into adjoining wooded areas. Hence its presence, and the absence of *Tamias*, would seem to require not only regional, but highly local grass cover.

The pocket gopher, *Geomys* cf. *bursarius*, has also been recovered from Savage Cave, Logan County, 150 miles southwest of Welsh Cave in presumed late Pleistocene, but highly disturbed, cave fill. Although *Geomys pinetus*, occurring in the pine woods of the South, approximately 400 miles south of Welsh Cave, is indistinguishable from *Geomys bursarius* on the basis of recovered fragments, the Welsh Cave specimens have been referred to *G. bursarius*, a decision weighted by the number of northern and western forms in the deposit coinciding with the absence of known southern forms.

The northern element in the fauna consists of water shrew (*Sorex palustris*), pygmy shrew (*Microsorex hoyi*), least weasel (*Mustela nivalis*), snowshoe hare (*Lepus americanus*), red-backed vole (*Clethrionomys* cf. *gapperi*), yellow-cheeked vole (*Microtus xanthognathus*), spruce vole (*Phenacomys* cf. *intermedius*), and probably the porcupine (*Erethizon dorsatum*) (although see Parmalee and Guilday, 1966). Water shrew, red-backed vole, and porcupine do, or did within historic times, occur in the Appalachian Mountains as far south as the Great Smokies. The remainder are primarily Canadian/Hudsonian Zone species of higher latitudes.

Of the 22 Recent species of mammals recovered from the fauna, 19 (water shrew, pygmy shrew, short-tailed shrew, common mole, badger, least weasel, snowshoe hare, cottontail rabbit, pocket gopher, woodchuck, 13-lined ground squirrel, red squirrel, red-backed vole, meadow vole, pine vole, porcupine, little brown bat, pipistrelle, white-footed mouse) have modern distributions that overlap in a small area of eastern Minnesota/western Wisconsin, directly south of the western tip of Lake Superior in the Transition/Canadian Life Zone ecotone, latitude 45°N., longitude 92°W.—about 7° of latitude and 775 miles northwest of Welsh Cave (fig. 31). Three Recent species recovered from the fauna are not recorded from this area. All are boreal or western. The spruce vole (*Phenacomys* cf. *intermedius*) occurs throughout the Canadian Life Zone, which lies to the north of the overlap zone, but its modern

southern distributional limits lie some 75 miles to the north of that zone (Hall and Kelson, 1959). The yellow-cheeked vole (*Microtus xanthognathus*), a Hudsonian Zone species, has not been taken in Recent times south of northern Manitoba, about 760 miles north of the overlap zone,



Fig. 31. Outline map of North America. Circled dot = Welsh Cave, Kentucky. S.O. = center of sympatric overlap of the range distributions of Recent members of Welsh Cave local fauna. a. = modern distribution of yellow-cheeked vole, *Microtus xanthognathus*. b. = modern distribution of plains pocket gopher, *Geomys bursarius*. c. = modern distribution of southeastern gopher, *Geomys pinetus*. Ranges adapted from Hall & Kelson, 1959.

although it was a common late Pleistocene inhabitant of the Appalachians as far south as Virginia. The original eastern border of the grizzly bear (*Ursus arctos*) is somewhat in doubt. Hall and Kelson place it approximately 50 miles to the west of the overlap zone.

None of the recovered species range entirely south or east of the overlap zone. The zone lies at or near the southern limits of the modern central North American ranges of the water shrew, pygmy shrew, least weasel, snowshoe hare, red squirrel, red-backed mouse, and porcupine, and at or near the northern limits of the short-tailed shrew, eastern mole, pocket gopher, pine vole, and cottontail rabbit.

It is noteworthy and probably significant that at Welsh and Savage caves, Kentucky, Robinson Cave, Tennessee, and other late Pleistocene cave deposits in the Appalachians south to Virginia and Tennessee, no mammals of modern southern distribution have been recovered. All late Pleistocene range changes to date have been either northern or western adjustments. Mexican free-tailed bat (*Tadarida brasiliensis*) remains from Mammoth Cave, Kentucky, are believed to be pre-Wisconsinan in age (Jegla and Hall, 1962). Either deposition was completed in these sites before maximum climatic adjustment took place or such southern forms never extended their ranges to the north during post-Wisconsinan times.

Although no area in North America today seems capable of sustaining the Welsh Cave fauna in its entirety, the Minneapolis/St. Paul region of eastern Minnesota and western Wisconsin seems most suitable in that respect. This area is a transitional one. Within the space of a relatively few miles several major biotic provinces meet—to form the Illinoian/Canadian Zone transition of Dice (1943) or the northern coniferous/easter deciduous/grasslands transition of Curtis (1959). Curtis's floristic boundaries were developed by superimposing range boundaries of 182 species of modern plants. A map of the major vegetation types in the Great Lakes region (Cushing, 1965:407) illustrates the rather abrupt vegetational change along an east-west transit from mixed conifer/hardwood forest in northern Wisconsin to savannah/parkland and prairie in western and southwestern Minnesota. Concerning such boundaries, Cushing states (p. 404) that "the degree of coincidence is remarkable considering the morphological diversity of the species represented. It must be concluded that in many cases plant migration is closely adjusted to climatic change, and that a quasi-equilibrium exists between the distribution of plant species and environmental variables. This point is



worth remembering when environmental interpretation of paleo-floristic data is attempted." This may also be said of animal communities, which in many cases have similar geographic boundaries. The numbers of herbivores, the ecological base of any terrestrial vertebrate community, are governed both quantitatively and qualitatively by vegetation types. Carnivores and insectivores that prey upon herbivorous elements of the biota form distinct communities coinciding with that herbivorous base. As a result, if such analyses are approached with caution, past climatic conditions may be legitimately inferred from the faunal composition of bone deposits like that of Welsh Cave.

The area of overlap points to a former condition of boreal semi-prairie or parkland in central Kentucky some 13,000 years ago—a condition affording more "ecological niches" than can be found in either pure grassland or closed forest. This assumes that all or most of the species recovered from the cave deposit were contemporaneous. The fact that there was no real stratigraphy at the site leaves this question an open one. We may have a heterochronous mixture of species that represent a time sequence ranging from prairie to today's closed forest situation. There is some evidence for intrusion. Contamination is believed to have been minimal. The fauna does appear to be ecologically plausible even in the light of present biotic distributions. Future operations at the site will undoubtedly add much to the picture.

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